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USE OF SHELLS OF FRESHWATER MUSSELS IN MONITORING HEAVY METALS AND ENVIRONMENTAL STRESSES: A REVIEW

Marc J. Imlay

ABSTRACT

Heavy metals which are dissolved in fresh water are partially removed from solution by freshwater mussels and are deposited in their shells during shell growth. Using proper techniques, annual shell growth increments can be detached from each other and analyzed, thus revealing annual heavy metal pollution events in the water. The mussels are thought to not move far and consequently are qualified for use as monitors of past or present heavy metal contamination at a site.

The purpose of this review is to recommend which species of mussels have shells and other physiological attributes that qualify them as best suited for monitoring pollution, what metals are concentrated in mussel shells, what the relation is between metal concentration in the environment and in the mussel shell, whether concentrations remain static in older annual growth increments, how far freshwater mussels move in their lifetimes, how one can reliably distinguish annual growth rests from disturbance rings, and whether the presence of disturbance rings is related to the degree of turbidity, pollution, low oxygen, low temperature or other adverse properties in the water.

Because of their widespread distribution, long life span, pollution tolerance and/or conchological reflection of stream location, certain freshwater mussel species are recommended as having shells which are of greatest utility for monitoring heavy metals and other environmental stresses. Cadmium, copper, lead, manganese, mercury, strontium, iron, magnesium, zinc, barium, sodium, silver and nickel all have been monitored in freshwater mussel shells, either whole or delaminated.

Two primary research needs are that concentration factors at different exposure levels be determined for the heavy metals in delaminated shells and that it be ascertained whether or not the concentration of a metal within an annual growth increment changes after the increment is covered by succeeding layers.

Freshwater mussels probably are not displaced downstream by winter storms, flash floods, etc., to an extent which would compromise their value as test organisms, but this needs to be confirmed by experimental tagging and monitoring over an extensive period of time. Significant factors that can cause downstream migration include temperature, water depth, lack of food, storms, and the shift from a juvenile to an adult habit.

The temporary disturbance rings probably are related to slug (acute and sublethal) doses of pollution and other environmental stresses.

INTRODUCTION

Freshwater mussels (naiads) in the United States consist of four species in the family Margaritiferidae and several hundred species in the family Unionidae. Freshwater mussels 15 years or older are found in most of our rivers and lakes. As the following review will show, the annual growth increments in the shell can be separated from each other in most cases and heavy metals are concentrated in the increments. The mussels are thought to not move far and consequently are qualified for use as monitors of past or present heavy metal contamination in the locations where they are found.

The purpose of this review is to provide information bearing on the following questions. Which species of mussels are best suited for monitoring pollution with shells? What limitations does variation among individual shells create? What metals are concentrated in mussel

shells? What is the relationship between metal concentration in the environment and in the mussel shell? Does concentration remain static in older annual increments? How much do freshwater mussels move in their lifetime? How can one reliably distinguish annual growth rests from disturbance rings? And, finally, can the presence of disturbance rings be related to such factors as the degree of turbidity, pollution, low oxygen and low temperature in the water? Because of the paucity of information on freshwater mussels, marine data was used to augment information concerning metal uptake.

FACTORS ASSOCIATED WITH MONITORING

Shell structure and methods of aging mussels

The freshwater mussels probably live the longest among freshwater invertebrates, 4-10 years among the thin-shelled pond species, but 20-40 years among the thicker-shelled river species. "A few hardy individuals are reported to have lived for nearly a century" (Stein, 1971). The distributions of species of *Unio* and *Anodonta* all show a "pattern of few young and relatively many specimens of the old age groups" (Pockendahl, 1976). This phenomenon appears to be almost universal among freshwater mussels (see, for example, Imlay (1972a), Stober (1972), concerning few juveniles and many older specimens). The following review of the literature has demonstrated that, with few exceptions, the major annual growth rest is easily differentiated from the more narrow temporary disturbance rings. The method of aging mussels by annual increment counts is perhaps 95% reliable.

There are five layers to the mussel shell. The outer periostracum is a thin proteinaceous layer which protects the inner layers from erosion and corrosion by low pH. The prismatic layer, peripheral layer, laminar layer, and the inner nacreous (pearly) layer are made up of aragonite and/or calcite, both crystal forms of calcium carbonate interspersed with a thin proteinaceous matrix. Mechanical properties of mother-of-pearl (nacre) were reviewed and experimented with by Currey (1977). Nacre is both a prismatic and also the strongest form of molluscan shell material, and consists of aragonite plates about 0.3 μm thick arranged in sheets with a thin protein matrix. White nacre is stronger than colored nacre, which in turn has a greater mean thickness. This strength may be why most of the inner mother-of-pearl layers of freshwater mussels appear to be white.

Coker et al. (1921) measured juvenile mussels for size and placed them in crates in the Mississippi River for over two years. They observed two annual rings and also a ring corresponding to the approximate date that they placed the mussels into the river. They demonstrated that a disturbed mussel would stop growing. The mantle edge which secretes shell material for the outer shell layers would retreat. After the mantle edge retreats from disturbance, it does not return exactly to its original position, but underneath. Thus there is a doubling or replication of the outer layers and a ridge is formed. The ring is not distinguishable on very dark colored shells such as *Fusconaia ebena* (Lea), *Quadrula pustulosa* (Lea) and *Amblema peruviana* Lamarck. The difference between the annual rings and disturbance rings is simply that the annual rings consist of a series of temporary disturbance rings caused by episodes of low temperature in fall and spring.

An incandescent light bulb, monochromatic yellow light, or ultraviolet light, as described by Chamberlain (1931), occasionally is necessary to determine the number of annual growth rests. Since the distance between annual growth rests decreases logarithmically with age, Chamberlain found it possible to extrapolate and determine the time of year of death. One other detail was found necessary for age determination (Pruiksma, 1978): scrubbing with a firm-bristled toothbrush and common kitchen scouring powder.

Imlay & Paige (1972) grew *Amblema plicata* Say in the laboratory. They were collected on 3 November in Minnesota, when the river temperature was 4.6°C. Growth was reflected

in new (third) annual growth increments. Isely's (1914) study of about 900 North American freshwater mussels which were tagged and later recovered showed that the annual increments were generally regular and definite enough for age determination. Ray (1977) used the acetate peal technique to analyze growth in freshwater mussels to test Chamberlain's microscopic conclusions. Mussels from the Buffalo, White and St. Francis rivers in the Ozarks were embedded in dental stone, cut at right angles to the growth increments, etched with HCl, and sometimes stained with Alizarin Red-S.

Ray concluded that both the annual rings with several duplications of the outer shell layers and the disturbance rings with single duplications were apparent. There was difficulty, however, "in attempting to distinguish between those two markers in all of the specimens analyzed." Negus (1966) had no trouble distinguishing disturbance rings from annual rings. In her studies she proved that the annual rings were formed in winter with marking and recapture experiments to demonstrate the time of ring formation. Grier (1922b) found that lake species showed more regular and distinct bands than did the same species in streams.

Taxonomic considerations in aging mussels

Margaritiferidae. Stober (1972) determined that the average age of *Margaritifera falcata* (Gould) in Madison River, Montana, was 47.9 years. The minimum and maximum ages were 10 and 67 years. In order to measure the older mussels, it was necessary to measure four young mussels and obtain a growth curve of the hinge ligament. Stober used the more reliable ligament annuli of older specimens and added the number of annual layers of existing noneroded recent ligament to the equivalent growth curve for the ligament of young specimens. This method also would work for *M. margaritifera* (Linnaeus), *Cumberlandia monodonta* (Say), and possibly *M. hembeli* (Conrad), the other three species in the family Margaritiferidae in the United States[2].

Unionidae. Anodontinae. Heard (1975) studied *Anodonta wahlametensis* Lea from California, *A. grandis corpulenta* Cooper from Arizona, and *A. gibbosa* Say, *A. hallenbeckii* Lea, *A. imbecilis* Say, *A. peggyae* Johnson and *A. couperiana* Lea from Florida and Alabama. The maximum age was 16 years in *gibbosa* and *hallenbeckii*, 15 years in *peggyae*, 11 years in *wahlametensis*, 13 years in *imbecilis* and *couperiana*, and 8 years in *corpulenta*. The oldest individuals of all these species were active in gametogenesis, and most of the oldest females were gravid.

Lampsilinae. St. John (1974) found that all populations of *Actinonaias ligamentina* (Lamarck) from Tennessee, Kentucky, Ohio and Oklahoma showed the most rapid growth in the second or third year, declining rapidly to the 10th year and then declining slowly after that. The largest individual was at least 40 years old. Bedford et al. (1968) monitored pesticides in Michigan streams with several species of freshwater mussels that were 20 years old where found.

Ambleminae. Magnin & Stanczykowska (1971) found *Elliptio complanata* (Lightfoot) and *E. dilatata* Rafinesque to live 15 years and *Lampsilis radiata* (Gmelin) to live 12 years in the St. Lawrence River channels. Yokely (1972) found that *Pleurobema cordatum* (Rafinesque) lived 25-30 years, at which time it was still reproductively functional. Scruggs (1960) found that in the Tennessee River in Wheeler Reservoir and Chickamauga Reservoir the age was determinate to 25 years. Individuals 27-29 years old or 30-32 years old could be determined within two years of age. Most extant mussels were 10 to 32 years old, although Isom (1969) verified the elimination of most species of mussels from behind the reservoirs.

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[2] *Margaritifera hembeli* lives in a mild climatic belt and might not show strong seasonal changes in growth rates.

Stansbery (1967, 1970) showed that older specimens of *Amblema plicata* in Lake Erie that had been stunted in growth simply continued to grow more in later years. Little & Gentner (1970) had problems with determining age of *A. plicata* in Little Brazos River, Texas. Some individuals grew in weight but not in size from 7 April to 16 September, presumably due to soft part growth only. Read (1954) found that several species in the Trinity River, Texas, laid down "good, solid, interruption rings when removed from their natural habitat and placed in aquaria. We may well believe that undisturbed clams in this region of abrupt climatic changes sometimes lay down two good interruption rings per annum – especially mussels of the shallow-water creeks and sloughs."

Downstream migration

Freshwater mussels probably are not displaced downstream by such events as winter storms and flash floods to an extent which would compromise their value as test organisms. But this needs to be confirmed by experimental tagging and monitoring over an extensive period of time, because mussels are most useful to monitor if they do not migrate much. Evidence not supportive of significant migration is presented first in the sections below, followed by more supportive evidence. Isely (1914) examined 164 "Quadrulae" in Oklahoma for migration a year after artificial displacement into Shoofly Creek from the Chikaskia River. He recovered 84.8% of the original tagged mussels and showed little, if any, migration. Forty-six percent of *Anodonta grandis* Say were found in their original location.

Imlay (1972b) placed 20 large *Lampsilis ventricosa* Barnes on their sides in 3 ft of water at one location near the bank in Eau Claire River, Wisconsin. Nineteen of these mussels were found in the same 4^2 ft placement area 1½ months later. Fifty mussels left on their sides in a 4^2 ft sandy area did not migrate over winter.

Coker et al. (1921) pursued the possibility that freshwater mussels locomote in order to transfer sperm. It was observed that male mussels in aquaria traveled extensively over the bottom, discharging sperm in a long winding furrow.

Another factor causing migration is the absence of food. Bovbjerg (1957) reported that *Lampsilis radiata siliquoidea* (Barnes) moved 2.3 m per week when fed algae, but between 3.4 and 6.7 m per week when not fed. Thus movement of 300 m per year or 3000 m in a decade in an oligothropic (absence of food) upstream location is possible.

Isely (1914) placed in shallow water (1 ft) mussels which always moved until they reached deeper water, 2 to 3 ft deep. Van der Schalie (1938) found that marked mussels do not migrate into deeper water during winter in the Huron River, Michigan, whereas Evermann & Clark (1917) found that they migrate into deeper water during winter in an Indiana lake. Read (1954) found that heavy shelled mussels migrated. Some were found in 6 in of water in Parson's Slough, Texas, but when the air temperature rose to 100°F they migrated to a quiet pool nearby where the water was 3 to 4 ft deep. Thin shelled mussels moved up or down in the upper 18 in of soft mud or sand. Matteson (1948a,b) placed marked *Elliptio complanata* in relatively deep water in late summer or early fall. They usually returned to water 3-5 ft deep in the following spring. Those placed in shallower water also migrated to 3-5 ft. Water warmer than 24°C caused them to migrate.

Matteson (1955) reported that "In a river system there is a tendency toward increased movement among mussels as the headwaters are approached. This is especially true where the current is definite, the water clear and shallow, and the bottom composed of sand or a mixture of sand and gravel. In this situation there would be a paucity of planktonic food, the water temperature would be highly variable, and the clam is able to move easily through the bottom materials. As conditions are usually more static in the lower reaches of a river there is less reason for movement."

Van Cleave (1940) observed the mussel fauna of the Salt Fork of the Vermillion River, Illinois, for 10 years. Collections in water from a few inches to 2 ft showed *Alasmidonta*

complanata fluctuating from 11.2% of the entire sample to 3.6% in one week, back to 9% the following year. A drop of 10°F occurred in air temperature that week, and the drop in temperature in shallow water may have brought about migratory movements toward deeper water.

Two factors are considered more significant than temperature, depth and lack of food in causing downstream migration: storms and the shift from a juvenile to an adult habit. The southwest side of Pelee Island, Lake Erie, is subject to violent wave action during storms (Brown et al., 1938). There was considerable mussel depletion. "Many dead clams (with bodies still attached) were found in the shore drift."

Little & Gentner (1970) marked and measured 190 mussels in the Little Brazos River, Texas. Five months later, after a careful search, 45 marked mussels were found. Unmarked mussels new to the pool also were found. Most of the 45 mussels were larger ones, indicating that smaller mussels (under 50 g) were unable to reestablish themselves or were dislodged more readily during a flash flood.

Roscoe & Redelings (1964) observed that whole beds of *Margaritifera margaritifera* had been washed downstream by natural storms into two new areas.

Imlay (1972b) reported that a collection over a 100 m stretch on the Eau Claire River, Wisconsin, yielded several species in large numbers, even though these species had been extirpated from that location 2 years earlier. It is not known whether the repopulation came from downstream or upstream, but it evidently represents a natural displacement from somewhere else in the stream.

Grier (1922a) noted that an apparent effect of the flood stage of the Mississippi River was to cause a migration of the mussels shoreward. Many mussels, especially juveniles inhabiting sandbars, died in large numbers because they were not able to move with the water as it dropped after the flood.

Valentine & Stansbery (1971) reported that thin-shelled species such as *Anodonta, Potamilus* (= *Proptera*), *Leptodea, Ligumia, Toxolasma* (= *Carunculina*) and *Lampsilis* tended to follow the rise and fall of fluctuating water levels if the mud or sand was soft enough. They described a thunderstorm at Glover Creek, Oklahoma. About 15 to 20 ft wide and up to 4 ft deep, Glover Creek rose to 6 ft in 15 min, "flowing in a rolling torrent bank to bank about 200 feet wide with large uprooted trees sweeping down the channel." The effects of the flash flood included hundreds of live mussels which were found incompletely buried. They could have been washed down from upstream.

Matteson (1955) found that during flood stage the surface of the water in an Illinois stream was 17 ft higher than normal. Any mussel occupying the bottom was subject to scouring and silting. A winter supply of *Alasmidonta calceolus* (Lea) was "swept down the creek although it was contained in a well-built anchored cage." He reported that *Anodontoides ferussacianus* (Lea) was able to withstand the powerful currents. He pointed out that the spines of the spiny mussels (*Canthyria* Swainson) prevent the animal from rolling along the bottom. Some species of *Anodonta* float on the water surface. Extreme lightness in weight and holding the valves tightly closed for extended periods of time are two adaptions used to combat silt. A floating mussel is likely to passively migrate, of course.

Matteson (1955) summarized for *Strophitus rugosus* (Swainson), which is found in large creeks, as follows. "If any of these mussels were to be uncovered by unusually strong currents such as those present during a stage of flood, they would be carried down the stream for varying distances. Eventually, they would roll into an area where currents were eddying in such a manner that downward progress would be halted. This reasoning would seem to show that the area formerly occupied by them would become depleted of these species, but it must be remembered that, simultaneously, clams from higher up the creeks will take their place, infected fish will drop young individuals, and the population will remain constant."

As for the shift from a juvenile to an adult habitat, Imlay (1972a) related the chance dispersal of host fish to the limited distribution of juvenile mussels. Coker et al. (1921) observed that in the experience of all collectors juvenile mussels are extremely difficult to find

except for occasional rich beds in particular locations. Juvenile mussels actually bury themselves in the bottom more deeply than do adults (Coker et al., 1921).

D'Eliscu (1972) noted that Isely (1911) and D'Eliscu (1970, unpubl. data) showed that few or no juveniles lived in the adult habitat. He also noted that juveniles are difficult to find. Juveniles of some mussel species have byssal glands and inhabit loose gravel, whereas their adults inhabit deep mud or sand. In conclusion, he stated that "the morphology, physiology and difficulty of collection of the juvenile stage seem to indicate occupation of an entirely different habitat from that of the adult." Negus (1966) likewise found that juvenile mussels occupy fewer kinds of habitats (silt-free but with organic materials) than do adult mussels.

Read & Oliver (1953) found early juveniles (5-17 mm long) of several species in Dallas County, Texas, only on gravel shoals attached by a byssus thread or an algal filament. He found *Anodonta* and *Leptodea* in the late juvenile stage in mud bottoms characteristic for adults.

A critical research need is to ascertain the presence of mother beds of mussels, both adult and juvenile. This would not only reveal migration from the juvenile to the adult habitat, but also help determine critical habitat of endangered mussel species.

Species useful for monitoring

Some species are useful for monitoring purposes because of their conchological reflection of stream location. If there is doubt about downstream migration, one can select for monitoring purposes certain species which increase regularly in obesity (total width of the two valves) in a downstream direction. These include *Amblema plicata, Cyclonaias tuberculata* (Rafinesque), *Fusconaia barnesiana* (Lea), *F. cuneolus* (Lea), *F. edgariana* (Lea), *F. flava* (Rafinesque), *F. subrotunda* (Lea), *Lexingtonia dolabelloides* (Lea), *Obovaria subrotunda* (Rafinesque), *Pleurobema coccineum* (Conrad), *P. cordatum, P. oviforme* (Conrad) and *Quadrula pustulosa* (Lea) (Ortmann, 1920; Ball, 1922). Although not much difference is observed in obesity, this last named species does not generally frequent smaller streams.

Quadrula metanevra (Rafinesque) is compressed in small streams and also loses its peculiar characteristic large knob sculpture. In the headwaters of the Ohio and Tennessee rivers, *Q. cylindrica* (Say) is compressed and smooth, having lost large knobs. In the headwaters of the Ohio River, the nodules are lost but are even more abundant in the upper Tennessee River than is the normal form. *Dromus dromus* (Lea) is swollen in the main river, but is the compressed *caperatus* (Lea) form in the headwaters. The flat form loses the hump, which is well-developed in the swollen form. Some of the moderately swollen individuals have no hump and some of the flat individuals have a trace of a hump.

Other species are useful for monitoring purposes because of their distribution and age.

Margaritiferidae. *Margaritifera margaritifera* has the widest range of any naiad in the world. *M. margaritifera* has a Holarctic distribution that includes Northern Europe, Iceland, and the eastern seaboard of North America from Labrador to Pennsylvania. *M. falcata* is west of the Rocky Mountains from Alaska to California. A relative of *M. falcata* occurs in northern Asia and Japan. Trout streams are the most favorable habitats for *Margaritifera*, and it is found in lakes in England and Europe. It is found in the arctic coast of Europe, where summer water temperatures reach only about 13°C. *Margaritifera* was absent from areas in Europe that were high in calcium. It is found in Scotland where calcium is 1-79 mg/l. In the south of England it is not found where the calcium is 70-115 mg/l. It is found in the Connecticut River system, where pH is 7 and $CaCO_3$ averages 26.5 mg/l (Smith, 1976) and maximum age rarely exceeds 23 years. The genus is recommended for heavy metal monitoring studies because of its long life throughout its range and its unique habitat and widespread distribution. *Cumberlandia monodonta* and *M. hembeli* are threatened or endangered; consequently, only recently dead shells may be used.

Ambleminae. *Amblema plicata* is a long-living unionid mussel which is recommended for monitoring purposes because it is widespread (Burch, 1975) and is more tolerant of pollution than most mussels (Imlay, 1971, 1973; Starrett, 1971). Thus it is especially useful where other species may be absent.

Elliptio complanata is the most widespread of the East Coast mussels occurring in both polluted and unpolluted waters and lotic and lentic habitats from Maine to Florida[3]. It may be recommended for monitoring purposes. However, other species live longer.

HEAVY METAL CONCENTRATION IN ANNUAL GROWTH INCREMENTS

Field surveys

Cadmium, copper, lead, manganese, mercury and strontium were greatly concentrated in freshwater mussel shells collected from various points along 200 miles of the Kentucky River (Williams & Powell, 1974). The concentrations in the mussels tended to be slightly higher in the middle portion of the river. However, the smaller ions of iron, magnesium and zinc were not highly concentrated.

Atomic absorption was used for the analysis. The digestion and atomic absorption procedure yielded results reproducible within 1-2% of samples containing known amounts of zinc, copper, manganese, strontium, iron and magnesium. Cadmium, lead and mercury yielded 5% reproducibility.

Cadmium shell concentrations were nearly 100 times higher than the concentrations found in soft parts, copper 6 times, lead 450 times, and manganese 1 time. This latter concentration, 212 mg/kg manganese, however, is several hundred times higher than for fish muscle. Copper in shells was 24 times more concentrated than in fish. Mercury appeared as 699 mg/kg in mussel shells. Strontium in the shell (467 mg/kg) was more concentrated than in mussel soft parts (0.7 mg/kg) and fish (0.1 mg/kg). Zinc was 6 times more concentrated in mussel soft parts than in fish, and zinc concentrations in mussel shells were 2-4 times lower than in soft parts. Magnesium was 10 times lower in shell than in soft parts. Iron was 10 times higher in mussel soft parts than in fish. Iron in mussel shells was approximately the same as in soft parts. The species tested were *Actinonaias carinata, Amblema plicata, Fusconaia ebena, Lampsilis anodontoides* (Lea), *L. fallaciosa* Smith, *L. radiata siliquoidea, Lasmigona costata* (Rafinesque), *Megalonaias gigantea* (Barnes), *Pleurobema* spp., *Proptera alata* (Say) and *Quadrula quadrula*. Williams & Powell delaminated the annual growth increments, digested them in nitric acid, and analyzed them by means of atomic absorption. The year in which high and low concentrations occurred varied. Williams & Powell argued that it is necessary to "ascertain whether or not the concentration of a particular metal within the laminae changes after it is covered by the succeeding layer." Waele (1930) concluded that *Anodonta cygnea* (Linnaeus) loses calcium when on a calcium-poor diet. The shell served as a calcium reserve, presumably for buffering products of glycolysis during anaerobiosis. One could drill a hole halfway through an annual ring, return the live mussel to the water, wait several years, analyze the drilled half and undrilled half, and determine if the metal concentration had increased or decreased in that time. An indication that it does not change may be found in the archeological investigations of Nelson and others concerning the calcium/strontium ratio.

Nelson (1964) analyzed freshwater mussel shells from the Tennessee River system by sawing them with a hacksaw, polishing with number 320 grit emery cloth, viewing with a dissecting microscope, and ashing in a muffle furnace at 400°C for 4 hr to destroy organic matter.

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[3] According to the immunoelectrophoretic findings of Davis et al. (1981), *Elliptio complanata* is likely a composite of several conchological sibling species.

After cooling, the layers were readily separated along the growth lines by inserting a scalpel. He found that with most species the strontium concentration was about 25% greater in the recent annual layers, but that the year in which this change took place was not the same for all species. He concluded "strontium concentrations in the prismatic and peripheral layers were approximately equal but the annual peripheral layers contained an average of only 77% as much strontium as did the corresponding laminar layers. Strontium concentrations were relatively constant in the annual peripheral layers. There was as much as a 100% difference in the strontium content of annual laminar layers which was related to age of the clam at the time the layer was deposited." Thus it is necessary to be consistent in the part of the annual growth increment that is analyzed, as well as the age of the clam, for a particular year.

Nelson (1967) found that Indian midden shells over 1,000 years old contained consistently higher concentrations of strontium than did living individuals. This difference was traced to changes in climate (Lee & Wilson, 1969) for the Big Sioux River, Iowa (Kimball and Phipps sites). There was a decrease in strontium/calcium ratio with increased discharge of the rivers. A modification of the procedures developed by Nelson (1964) was used in the separation and analysis of the annual growth increments for calcium, magnesium and strontium. The strontium/calcium ratio coincided with the secondary climatic optimum, the Little Ice Age, and the present conditions.

In the 1967 paper, Nelson analyzed strontium, barium, magnesium, manganese and sodium uptake in the annual growth increments of eight species. Strontium and barium were more highly concentrated in the laminar layers than in the peripheral layers of all eight species. The more recently deposited annual laminar layers had more strontium and barium in seven of the eight species. *Elliptio dilatata* had less strontium and barium in the most recent layers; its microhabitat is different than that of the others, however. Manganese increased in both the recent peripheral and recent laminar layers for *Plagiola lineolata* Rafinesque and *E. crassidens* (Lamarck). Sodium was the same in the peripheral and laminar layers. Species differences included a variation in strontium from 120 μg/g in *Anodonta corpulenta* to 620 μg/g in *Actinonaias carinata*, a barium maximum in *E. dilatata* and a minimum in *Lasmigona complanata* (Barnes), and manganese from 100-150 μg/g in several species to 2,500 μg/g in *L. complanata*.

Working on *Amblema plicata, Lasmigona complanata, Obliquaria reflexa* Rafinesque, *Potamilus* (= *Proptera*) *alatus* (Say) and *Quadrula quadrula* collected in the Muskingum River, Sterrett & Saville (1974) chose activation analysis because of its sensitivity to metals and because it required only a small amount of sample material (0.5 g). They had better success with Pahl's (1969) method using 500°C for 10 min than with Nelson's method using 400°C for 4 hr.

Saville & Sterrett (1974) found no significant sex difference in *Amblema plicata* in the uptake of calcium, manganese and sodium, whether for 3-year olds or 7-year olds. There were no age differences with calcium or sodium in *A. plicata* and *Quadrula quadrula*. However, manganese increased with increasing age. Pruiksma (1978) employed neutron activation on the second annual peripheral layer in five species of different ages. There was a significant difference in manganese concentration between 4-year old specimens of *Q. pustulosa* collected at Beverly and collected at Lowell on the Muskingum River, Ohio. A significant difference also existed between 6-year old *Obliquaria reflexa* collected at Beverly and those collected at Lowell.

Fimreite et al. (1971) found mercury concentrations of 1-4 μg/g in freshwater mussels near pulp mills and chlor-alkali factories. Smith et al. (1975) sampled mercury in Minnedosa Lake, Manitoba, and Clay Lake, Ontario, in water, sediments and mussels. Mercury in Clay Lake was 20 times greater than in Minnedosa Lake in the water and 10 times greater in wet sediment. Mercury was 10 to 20 times as high in *Anodonta grandis, Lampsilis radiata* and *Lasmigona complanata* in Clay Lake than in Minnedosa Lake.

Mercury was analyzed in *Anodonta anatina* (Linnaeus) in Great Britain with atomic absorption and flameless cold vapor technique; and zinc, nickel, lead, cadmium and copper with atomic absorption and a dueterium background corrector (Manly & George, 1977). Zinc, nickel, lead and cadmium were elevated in *A. anatina* in urban localities, whereas copper and mercury were highly concentrated in mussels from rural areas where copper and mercury compounds are applied as pesticides. In summary, "*Anodonta anatina* appears to have some value as an indicator of heavy metal pollution. It can accumulate substantial quantities of all the metals studied here and there is evidence to suggest that the extent to which it does so is related to the levels of these in the environment."

Uptake studies

When *Anodonta californiensis* Lea was exposed for five days to ^{65}zinc, the shell took up more zinc than the mantle and less than the gills, after 3, 8, 16 and 36 days (Pauley & Nakatani, 1968). ^{65}Zinc fixation by *A. cygnea* was proportional to the ^{65}zinc concentration in the water (Foulquier et al., 1973). In a second experiment, water in an aquarium containing sediment was contaminated with ^{65}zinc. After 59 days, water contained 0.2% of the quantity of ^{65}zinc, *Anodonta* 6.2% and the sediment 93.6%. The concentration factor was 230x between water and shell and 3220x between water and soft parts.

Anodonta piscinalis Nilsson was exposed for 125 days to ^{32}phosphorus, ^{137}cesium, ^{89}strontium, ^{144}cerium, ^{95}zirconium, ^{95}niobium and ^{103}ruthenium (Garder & Skulberg, 1965). Water was pumped from a nearby river with the same temperature variations as those in the river and a natural food supply. Calcium and strontium are taken up from particulate food in the gut but also directly from the water (Bevlander, 1952; Fretter, 1953; Rao & Goldberg, 1954; Kado, 1960). The concentrations of the radionuclides "were extremely small so that the solubility products were not significantly affected by the addition; and the radionuclides did not precipitate" (Garder & Skulberg, 1965). After one month's exposure, a level of radioactivity was reached in the shell which was nearly constant with only slight fluctuations during the rest of the experiment. The concentration of ^{32}P was 5855×10^{-4} μ Ci/g ash weight of the body and 5.6×10^{-4} μ Ci/g ash weight of the shell; ^{89}strontium, 933×10^{-4} body and 7.0×10^{-4} shell; ^{137}cesium, 281×10^{-4} body and 9.5×10^{-4} shell; ^{144}cerium, 800×10^{-4} body and 11×10^{-4} shell; ^{95}zirconium and ^{95}niobium, 142×10^{-4} body and 3.4×10^{-4} shell; ^{103}ruthenium, 33×10^{-4} body. Concentrations in the water were 1 to 8×10^{-6} μ Ci/ml.

Fikes (1972) maintained *Amblema plicata* in the laboratory. When the iron content of the water was high (0.3-0.8 mg/l), the pseudofaeces (egested material) were dark red like iron oxide. Hobden (1970) injected $^{59}FeCO_3$ into the visceral mass of *Elliptio complanata*. The radioactivity took up to one day to disappear from the blood. The injected iron was excreted very slowly if at all. A special type of pigmented cell appeared to store the iron in the gills and mantle. Starved mussels lost soft tissue far more than iron. "A partial alternative to this explanation is that some of every naturally occurring element must enter the animal with its food. If no adequate excretory mechanism exists as in the bivalve molluscs the element will accumulate probably in a bound or insoluble form."

Terhaar (1977) exposed *Ligumia* sp. and *Margaritifera margaritifera* to 0.5 mg/l of silver and 2 μg/l of mercury at 18-21°C. At seven weeks, silver in the soft parts reached a maximum of 4.0-4.1 mg/kg and mercury was 100-125 μg/kg. At 10 weeks, silver was down to 2.9-3.3 and mercury held at 110-118. With 5 mg/l of silver and 5 μg/l of mercury, silver again was maximum at seven weeks. However, it was more than 10 times greater, being 66-110 mg/kg. Mercury at 5 μg/l was approximately twice as great as at 2 μg/l but irregular.

Chaisemartin (1977) was interested in freshwater mussels as indicator organisms because they live in sand and mud and water, cannot avoid collecting a series of heavy metal ions which adhere to the mucus, and feed on suspended particles and microorganisms. Twenty

live *Margaritifera margaritifera* were introduced in tanks containing 50 l of water and 10 l of sediment maintained at 16°C. The pH was maintained at 6.9 ± 0.2, because at that pH copper is essentially in a free ionic form. In the presence of sediment, a significant portion of the metal has the property of diffusing into the interior of crystalline grains of certain clays. Copper chloride was added with and without suspending the sediment. With suspension, the mussels took up more than twice as much copper over 10 days. Furthermore, the shell took up 38% of the copper with material in suspension. The soft parts took up 62%. Without suspension, the shell took up 16% and the soft parts took up 82% of the copper.

Short et al. (1969) measured the uptake of ^{131}I by *Margaritifera margaritifera* in Fern Lake, Washington. The shell accumulated three times as much as the soft parts in 29 days – considerably more than fish and considerably less than crustaceans. "The carapace of the crayfish, the shell of the clam, and the thyroid of the trout were respectively the tissues with the highest concentrations."

Salanki & Varanka (1976) exposed *Anodonta cygnea* to $CuSO_4$, $PbCl_2$ and $Pb(NO_3)_2$. At concentrations of 10-100 μg/l $CuSO_4$, "The duration of the active periods became shorter. The duration of activity reached only 5-20% of the control." The threshold was 0.01 μg/l. "According to our data the presence of 10^{-8} g/l $CuSO_4$ is already harmful in this respect. At 1 mg/l $Pb(NO_3)_2$, the decrease in the duration of active periods was about 10% . . ."

How can bivalves accumulate so much and yet be so sensitive to small quantities of heavy metals? "Oysters tolerate tissue residues of DDT at least as high as 150 mg/l without apparent ill effect provided residues are accumulated slowly. However as little as 0.1 mg/l of DDT in the oysters' water supply terminates feeding activities and at summer water temperatures (31°C) will cause death" (Butler, 1973).

MONITORING ENVIRONMENTAL STRESSES WITH DISTURBANCE RINGS

The narrow disturbance rings may be related to slug (acute and sublethal) doses of pollution and other environmental stresses. Thus they need to be examined for their intrinsic monitoring value as well as their distinguishability from annual rings. These rings in Wisconsin mussels, approximately 1-4 per year, were evidently caused by floods, droughts, and storm disturbances (J.P.E. Morrison, pers. commun. 1967). Shuster (1951) reported that the mid-season checks in the shell of *Mya arenaria* Linnaeus correlated with storms in Delaware Bay, New Jersey, apparently as a reaction to the presence of fine particles of silt which lodged between the periostracum and the shell. In the laboratory, silt produced a check (cessation of growth) in the shell. Agitation with a mechanical stirrer alone had no effect. J.C. Williams (pers. commun. 1973) found that crowfoot bars would not catch mussels as soon as the water became turbid. Evidently, mussels close up in turbid water. Crowfoot bars were ineffective for as long as three months one summer. Commercial musselers reported the same phenomenon. Ray (1977) noted that the overlapping or doubling up of the outer two shell layers in freshwater mussels may be a result of extreme water temperature fluctuation, or temporary stranding of the mussel. Coker et al. (1921) found that whenever a mussel was taken out of the water, measured, and put back in the water a ring would be formed. Chamberlain (1931) found that the degree of overlapping of layers appears to depend on the degree of the disturbance. Ellis (1936) employed automatic glass stirrers which created currents that suspended silt in experimental tanks. He found that "Mussels in muddy water remained closed 75-90% of the time. Mussels in silt free water were closed less than 50% of the time."

Wisely & Blick (1967) exposed larvae of *Mytilus edulus* Linnaeus and *Crassostrea commercialis* (Iredale & Roughley) to copper and mercury. High resistance occurred due to withdrawal of the larvae into their shells for the 2 hr of exposure. Imlay & Paige (1972) indicated that freshwater mussels required at least 4.5-6.4 mg/l dissolved oxygen for unimpaired

growth, and perhaps as much as 6.0-8.4 mg/l. Ellis (1936) verified that for small amounts of organic material mixed with erosion silt, oxygen demand was increased 10-15 times as with the same amount of organic material with fine sand instead of silt.

Loosanoff & Tommers (1948) found that a filtrate of *Chlorella, Nitzschia* and *Euglena* cultures containing metabolic wastes, or the cells themselves, or 0.1 g/ml kaolin (aluminum silicate) reduced the rate of pumping 57%. The average rate of pumping decreased 94% in concentrations of 3 and 4 g/l of silt. "Although such heavy concentrations seldom occur in nature they may nevertheless arise during heavy floods or be created in areas where the bottom deposits are artificially disturbed as happens in the case of channel dredging."

Mussels may be collected from a polluted river which is monitored daily for pollutants, temperature extremes, siltation, low oxygen, turbidity and other environmental stresses. The presence of disturbance rings may demonstrate that certain conditions are unsatisfactory for the uninterrupted growth of the species. Such variants may be stunted in growth.

Mussels would be dated monthly by the method of Coker et al. (1921). A slug dose of pollution would be assayed and distinguished from ambient, prevailing parameters. One also can check for presence or size of crystalline styles for evidence that the mussel was or was not feeding during the investigation.

CONCLUSIONS AND RECOMMENDATIONS

1. Because of their widespread distribution, age, pollution tolerance, and/or conchological reflection of stream location, I recommend the following freshwater mussel species for monitoring heavy metals on the basis of annual shell growth (however, endangered forms, here marked with an asterisk, may not be used alive): *Amblema plicata*; *Fusconaia subrotunda, F. flava, F. cuneolus*, F. edgariana** and *F. barnesianus**; *Quadrula pustulosa, Q. metanevra* and *Q. cylindrica**; *Lexingtonia dolabelloides**; *Pleurobema oviforme, P. cordatum* and *P. coccineum*; *Dromus dromus**; *Obovaria subrotunda*; *Margaritifera margaritifera* and *M. falcata*; *Cumberlandia monodonta**; *Elliptio complanata*; and *Cyclonaias tuberculata*.

Choice of species for monitoring past trends will depend on their natural presence in the drainages being surveyed. Where possible, the more widespread species are preferred: Holarctic, *Margaritifera margaritifera*; Northeast United States, *M. margaritifera*; Northwest United States, *M. falcata*; Eastern United States, *Elliptio complanata*; Interior United States, *Amblema plicata, Cyclonaias tuberculta, Fusconaia flava, Quadrula pustulosa* and *Pleurobema coccineum*.

2. Freshwater mussels probably are not significantly displaced downstream by winter storms, flash floods, etc., but this needs to be confirmed by experimental tagging and monitoring by such means as miniaturized radio transmitters or tracers.

3. Cadmium, copper, lead, manganese, mercury, strontium, iron, magnesium, zinc, barium, sodium, silver and nickel all have been monitored in freshwater mussel shells, either whole or delaminated. There are species differences, age differences, and layer differences, but apparently no sex differences. In one study, the concentration of zinc in the shell was proportional to the concentration of zinc in the water. The concentration factor between water and shell was 230X. In a second study, mercury in soft parts was proportional to mercury in the water, although the concentration factor varied by about 50% over a 20-fold range in concentration in the water. In a third study, mercury in soft parts was twice as great with an increase of 2.5 times in the water. Silver in the soft parts increased 10 to 20-fold with a 10-fold increase in the water. These appear to be the only studies which are directly applicable to a monitoring program, and I recommend that concentration factors at different exposure levels be determined for the heavy metals in delaminated shells.

4. Although long-term instability of metals in annual growth increments is not considered likely, it must be ascertained with greater certainty whether or not the concentration of a

metal within an annual growth increment changes after the increment is covered by succeeding layers. An experimental field or laboratory method is described.

5. Mussels should be collected from a polluted river which is monitored daily for pollutants and temperature, dissolved oxygen, siltation, etc. An attempt should be made to correlate disturbance rings with such environmental stresses. The presence of disturbance rings would demonstrate that the conditions are unsatisfactory for the uninterrupted growth of the species.

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SOME CHARACTERISTICS OF A SPRING INCURSION OF *APLYSIA BRASILIANA* INTO SHALLOW WATER

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ABSTRACT

Sampling of a shallow water population of *Aplysia brasiliana* in South Florida indicates that an incursion into shallow water occurs during the spring. Stranding of *Aplysia* on beaches was least common during storms, suggesting that animals found near shore are not merely displaced there by wave action. A decline in the proportion of reproductively active large animals in the population as the spring progressed suggests that the incursion may be correlated with reproduction.

INTRODUCTION

The literature on opisthobranch gastropods contains many references to incursions or aggregations of individuals of a species in shallow water. These events often are described as occurring suddenly and being related to some aspect of reproduction (e.g., Hecht, 1895; Balch, 1908; Crozier, 1917; Wright, 1960). However, quantitative measures of abundance in an area before, during, and after a supposed incursion or aggregation have not been published, nor have data documenting the shifts in population structure that would be expected if such an event were related to reproduction.

Various biologists and fishermen have noted an apparent incursion of *Aplysia brasiliana* Rang into the shallow waters of southwest Florida in late winter or early spring during most years. Sightings of *Aplysia* swimming near the shore and in passes between islands, and of the many *Aplysia* stranded on beaches, regularly produce inquiries from the public during this period. While studying other aspects of aplysiid biology in southwest Florida during the spring and early summer of two years, we obtained data on stranded animals, and on animals collected near beaches, in order to determine if an incursion actually occurs during the spring and to document any associated changes in population structure.

METHODS

Observations were made in Placida Harbor, Charlotte County, Florida, throughout June, 1975, by H.W.A. and from 16 March to 13 May, 1979, by P.V.H. and B.J.R. During the former study period, some *Aplysia brasiliana* were collected while they were swimming in waters immediately surrounding Bird Key, particularly in Gasparilla Pass, and some were collected from beaches. During the latter study period, two sections of beach on Bird Key were surveyed for stranded *Aplysia* within 4 hr after sunrise on 20 different dates. These beaches were identified as SB1 (367 m long) and SB2 (240 m long) in the map of the study area included in Hamilton & Russell (1981a). Only one of the two sample beaches was surveyed on four of the 20 dates, so stranding incidence for each date is expressed in animals per meter surveyed. Only data from these beach surveys were used in the stranding incidence analysis. During the latter study period, some *Aplysia* were also collected while they were swimming in waters surrounding Bird Key. Data from all animals were used in the size-frequency analysis.

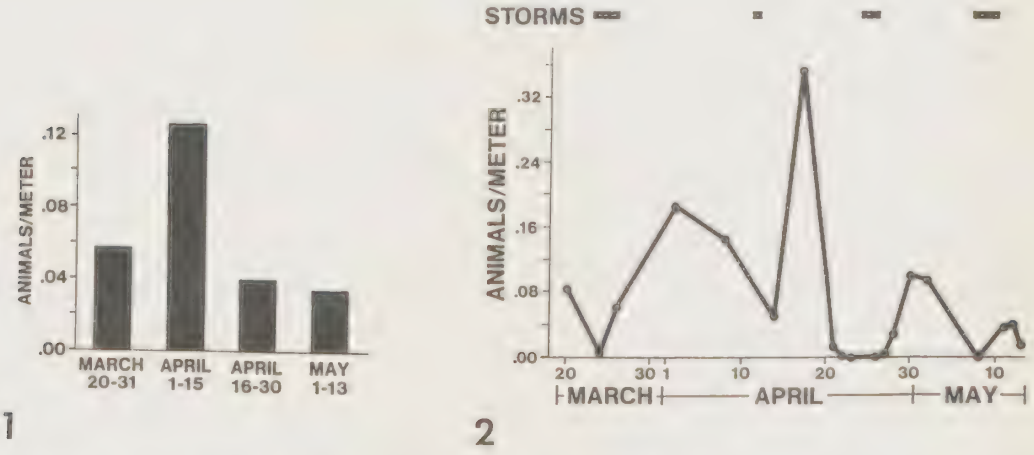
All live or recently dead *Aplysia* were collected and the volume of seawater each one displaced was measured to the nearest 5 ml. Volume was subsequently converted to mass using 1.044 gm/ml as the average density (n=17) of an *A. brasiliana*. Linear dimension was not used as a measure of size because body shape is temporally variable.

Voucher specimens have been deposited in the collections of the Mollusca Section, British Museum (Natural History), London (Registration No. 1974.23/1-8).

RESULTS

The number of *Aplysia brasiliana* becoming stranded on beaches is not uniform throughout the spring. Figure 1 shows the number of *Aplysia* stranded on the sample beaches during the 8-week period of 1979, grouped in four 2-week periods, and Figure 2 shows the data for each survey date. Figure 1 indicates a peak in stranding incidence during early April and suggests that *Aplysia* had started stranding on beaches before our 1979 beach sampling began (20 March). Area fishermen first sighted *Aplysia* on beaches during the last two weeks of February, 1979.

The influence of weather conditions is superimposed on the general trends in stranding incidence during the spring. Figure 2 indicates those days during which both the average barometric pressure was below average for the month and the average wind speed was above average for the month. The data were recorded by the National Weather Service at Fort Meyers, Florida, about 45 km ESE of the study area. Taken together, these climatological measures indicate major storm fronts which produced extended periods of higher-than-normal wave action. There were four major storm fronts during the study period, each coinciding with a major decline in stranding incidence for *Aplysia*.



FIGS. 1, 2. Number of *Aplysia brasiliana* stranded per meter of beach surveyed during spring, 1979. FIG. 1. Data grouped in four 2-week intervals. FIG. 2. Data for each of the 20 survey dates. Thick horizontal bars indicate the occurrence of major storm fronts.

A striking shift in population structure is associated with the spring incursion of *Aplysia* into shallow water. Figure 3 shows the size-frequency distributions of the 739 *Aplysia* collected during the 8-week period in 1979, divided into four 2-week periods, and a size-frequency distribution for the 110 *Aplysia* collected during June, 1975. During the last half of March, 1979, about two-thirds of the animals weighed more than 0.2 kg. These larger animals gradually became less common until, by the first half of May, 1979, only about one-third of the animals weighed over 0.2 kg.

No size difference between animals collected while swimming and while stranded on beaches was apparent. That stranded animals were not weakened post-spawn individuals is indicated by their rapid recovery when returned to water and successful use in behavioral experiments thereafter (see Hamilton & Russell, 1981a).

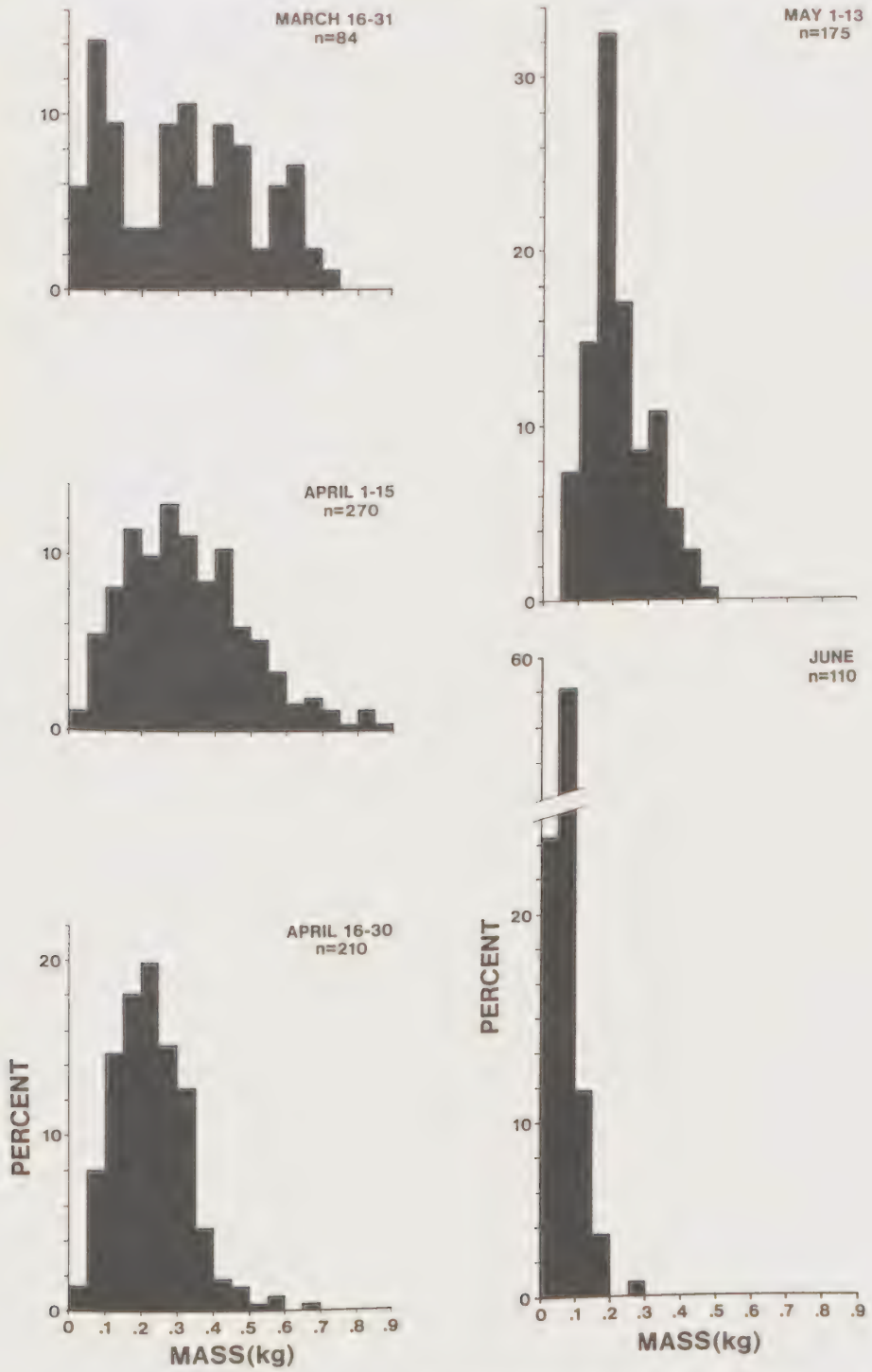


FIG. 3. Size-frequency distributions of *Aplysia brasiliana* collected near Bird Key during an 8-week period in spring, 1979, divided into four 2-week intervals, and a size-frequency distribution for animals collected near Bird Key during June, 1975.

DISCUSSION

There is evidence of a definite peak in the number of *Aplysia* becoming stranded on beaches (Figs. 1, 2). For the beach surveys conducted during the first two weeks of April, 1979, one *A. brasiliana* was encountered every 7.94 m of beach, on average. Our beach surveys in 1979 apparently began at least two to four weeks late. Krakauer (1969) surveyed Cedar Key beaches for *A. willcoxi* throughout the year and, although her sampling effort was somewhat irregular, a distinct peak in abundance was apparent during late February and early March; few or no animals were present on her sampling beaches before January or after May. *A. willcoxi* is a synonym for *A. brasiliana* (Strenth & Blankenship, 1978).

Eales (1921), Chambers (1934) and Carefoot (1967) speculated that *Aplysia* found in intertidal areas may have been displaced there by wave action during storms. Our data do not support this speculation. Although large amounts of molluscan shells, plant material and other debris washed ashore during periods of high wave activity resulting from storm fronts, the fewest *Aplysia* became stranded on beaches under these conditions (Fig. 2). These data were not influenced by observer bias, since all debris was carefully inspected to locate *Aplysia* possibly hidden underneath. Nybakken (1978) recorded the lowest abundances of nudibranchs during stormy weather but could not exclude observer bias as a possible cause due to the nature of his study area. *Aplysia* may burrow into the substrate during storms, thus avoiding displacement by wave surge. Burrowing has been reported for *Aplysia* (Aspey & Blankenship, 1976), although these authors speculate that the behavior may be related to physiological state.

It is unclear why *Aplysia brasiliana* strand on beaches in such large numbers. Both our observations and Krakauer's (1969) indicate that most animals become stranded by overnight high tides. Hamilton & Russell (1981a,b) found that both wave surge and visually detected celestial cues are used in the orientation of swimming during the day, so the general unavailability of these cues on calm nights may result in greater stranding. Conversely, the reduced incidence of stranding during storms may be due to facilitation of offshore-oriented swimming by the presence of large waves.

The size-frequency distributions in Fig. 3 show that, in the Placida area, the larger *Aplysia brasiliana* (>0.2 kg) which strand on beaches and swim in nearshore waters in the early spring gradually become less common as the spring progresses. Frequent observations of copulation and egg laying in the early spring suggest that these larger animals are sexually mature adults. The decline of animals larger than 0.2 kg in our samples as the spring progressed indicates that adults either died or moved out of the intertidal zone. The pattern of shift in the size-frequency distributions presented here is similar to that obtained by Krakauer (1969) at Cedar Key for *A. willcoxi*. During March she encountered the largest *Aplysia*; none were smaller than 0.1 kg and some were as large as 0.65 kg. During July and August she encountered the smallest *Aplysia*; none were larger than 0.15 kg. Krakauer's collection data spanned an entire year and suggest that *A. brasiliana* in Florida has a life cycle lasting about one year. Carefoot (1967) reported a similar sequence of size-frequency distributions and a 1-year life cycle for *A. punctata* on the British coast, although the changes there appear to lag behind the changes for *A. brasiliana* in south Florida by three to four months.

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STUDIES ON *TRICULA APERTA* AND RELATED TAXA, THE SNAIL INTERMEDIATE HOSTS OF *SCHISTOSOMA MEKONGI*. IV. CHROMOSOMAL STUDIES

Viroj Kitikoon

ABSTRACT

Chromosome cytology was studied in the alpha, beta and gamma races of *Tricula aperta*. Haploid chromosome numbers in males ranged from 13-17 in the alpha race and 14-17 in both the beta and gamma races. Alpha and gamma race females had the haploid chromosome numbers 16 or 17, and beta race females had 17. There was no variation in the beta females. Variation in chromosome pairing at male meiosis occurred. Twelve bivalents and a trivalent were seen in some alpha males, but not in males of the beta and gamma races; 14 bivalents, a trivalent and a univalent were seen in the gamma males, but not in males of the other two races. The basic haploid chromosome numbers appeared to be 13 in the alpha race and 14 in the beta and gamma races. The chromosome number 2n + 1 was seen in males only. The extra chromosomes of all three races of *T. aperta* may be related to sex determination. Males may have an XO chromosomal sex-determining mechanism and females may have XX.

Diploid chromosome numbers also showed variation. Beta females contained 2n = 34 chromosomes, whereas both the alpha and gamma races had both 2n = 32 and 34. Beta males had 2n = 31 and 33 chromosomes, while the alpha and gamma males had 2n = 29, 31 and 33. Karyotypes of the three races showed distinct morphological differences.

INTRODUCTION

The alpha, beta and gamma "races" of *Tricula aperta* seem to be qualitatively different in shell morphology and anatomical traits, as we have discussed previously (Davis et al., 1976), but we do not know as yet the taxonomic status of these so-called races. Are they simply populations of the same species, are they distinct subspecies, or are they reproductively isolated species?

Cytotaxonomic studies have proven useful for a long time to taxonomists interested in something more than simple morphological criteria for identifying (defining) species relationships. The karyotypes of different species usually differ in regard to chromosome shape and size, and often in number. Chromosomes have been studied in mollusks, especially in pulmonate snails, since the late nineteenth century, but not much progress was made for a long time because of inadequate microscopes and techniques. An increasing number of studies on molluscan chromosomes have been conducted in recent years. The relationships of chromosome numbers and systematics in certain taxa have been summarized by Burch (1965, 1967), Inaba (1961) and Patterson (1967, 1969).

Among the pomatiopsine hydrobioid snails, chromosome numbers of *Oncomelania*, the snail intermediate hosts of *Schistosoma japonicum*, were studied by Burch (1960) and Patterson (1963). They found that each of the four main geographic subspecies had 17 pairs of chromosomes. No one has previously attempted to study the chromosomes of the triculine hydrobioid *Tricula aperta*.

MATERIALS AND METHODS

The snails used in this study were field-collected from two isolated areas and maintained in the laboratory of the Mollusk Division, Museum of Zoology, The University of Michigan, as described previously.

The alpha race snails came from a pool at Ban Khi Lek (see E, fig. 9, in Kitikoon et al., 1981), the beta snails from site 7 at Phibun (see C, fig. 11, in Kitikoon et al., 1981) and the gamma race snails from site 3 at Ban Bung Kong (see C, fig. 9, in Kitikoon et al., 1981). The gonadial tissue (ovaries or testes) of mature snails were used for cytological studies, because this is the organ where active meiotic and mitotic divisions occur. The cytological preparations included spindle inhibitor treatment, tissue fixation and acetic-orcein squash procedures for temporary and permanent mounts, following the methods of La Cour (1941), Newcomer (1953), Patterson (1971) and Patterson & Burch (1978), with some minor modifications.

The shell of each snail (of known sex) was gently cracked with a scalpel under a stereoscopic microscope. Major damage to the vital organs had to be avoided in order to prevent death during the period of treatment with hypotonic solutions of sodium chloride and the spindle inhibitor. However, minor scratching of the surface skin of the gonadal tissues with a sharp needle was helpful for chemical absorption. Some pieces of crushed shell were carefully removed prior to treatment while the snails were resting in the conditioned water. These snails were then treated in three different concentrations of sodium chloride and spindle inhibitor (Velban, a trade name for vinblastine sulfate, Eli Lilly and Co., Indianapolis, Indiana, U.S.A.) solutions. Pooled groups of 20-30 snails were used in each treatment in order to get maximum use of the expensive Velban.

The treatment was carried out by the following procedure. The conditioned water was discarded from the watch glass with the aid of a hypodermic syringe or capillary pipette. The remaining water was then removed by absorbent paper. Ten ml of an isotonic solution of 0.04% NaCl and 0.00025% Velban (prepared from a stock solution of 1 mg/ml of vinblastine sulfate dissolved in bacteriostatic sodium chloride (injection solution) [which could be kept at 2-8°C in a refrigerator for 30 days without losing its potency]) were added onto the crushed snails in the watch glass and incubated for 3 hrs at room temperature (28°C). Then, ½ of the total volume of the solution was withdrawn using a hypodermic syringe and replaced with the same amount of 0.02% NaCl. The snails were kept in this solution for at least ½ hr before it was withdrawn. The procedure was repeated by adding a hypotonic solution of 0.025% NaCl and 0.0000675% vinblastine sulfate, in which the snails were kept for ½ hr prior to fixation. The hypotonic solution helped to keep the chromosomes loose and able to be easily spread when the squash procedure was performed.

During the last step of the above procedure and just prior to continuing the fixation, any dead snails were discarded. The testing procedure was to touch the base of the tentacle with the sharp point of a dissecting needle. If there was no movement or the tissue was pale and opaque, the snails were considered to be dead. The living snails were fixed by simply withdrawing the hypotonic solution from the third step and immediately replacing it with Carnoy's fixative or modified Carnoy's fixative (glacial acetic acid and 95% ethanol, 1:3 parts by volume). The amount of fixative solution used was at least 10 times greater in volume than the tissue. The fixing time varied according to the size and the condition of the tissue. The larger pieces of the tissue or those tissues containing lipid took longer to fix.

The stain was prepared by adding 2.2 g of Certified Synthetic Orcein (Matheson Coleman & Bell, Norwood, Ohio, U.S.A.) to 100 ml glacial acetic acid and bringing the mixture to a gentle boil for 10 min, with constant stirring or with the addition of glass beads. Usually, a more concentrated stain gave better results. Therefore, a longer period of boiling was preferred, i.e., until the volume of the solution had been reduced one half. The mixture was allowed to cool and was filtered through glass wool to remove undissolved stain. This stain gave excellent results.

Two different procedures for staining were used. In the single specimen staining procedure, each snail was stained singly. In male snails, the fixed testes were carefully dissected to exclude the vas deferens and the prostate gland, so as to minimize the amount of sperm and other debris which might cause interference during chromosome observations. The lipid in the ovary was removed by letting the tissues stand for a longer time in the Carnoy's fixative. The fixed gonadial tissue was then placed in the well of a depression slide or in a small vessel to which one or two drops of stain were added. Proper staining required 15-30 min, depending on the size and the condition of the tissues (e.g., tissues in which the surface had been scratched stained faster). The stained tissues were then removed and placed on a clean slide and a few drops of 45% glacial acetic acid were added to rinse off excess stain. The cover slip was then applied.

Since the snails used in the pooled specimen staining studies were all very small in size, their whole bodies were stained. Pooled, freshly fixed or preserved specimens of one sex were put into a staining jar and the fixative solution completely withdrawn. The amount of stain varied according to the number of specimens used. The stain always completely covered the specimens. Staining took 1-12 hrs, depending on the condition of the specimens and of the stain. Longer staining times gave better results for two reasons: the chromatin stained better and the acetic acid in the stain dissolved the calcium bits of shell that may have been embedded in the tissues. When the staining was completed, the stain was withdrawn and the excess stain was washed out with 45% acetic acid.

Observations of gametogenesis in various fixed cells were made under a binocular Nikon (Nippon Kogaku) microscope, using 100 (n.a. 1.25) oil immersion objective and 10X and 15X oculars. A Kodak 57A green filter, Kodak High Contrast Copy film and Kodak Polycontrast rapid F SC paper were used for photography.

RESULTS

Snails of each race of *Tricula aperta* to be used for cytotaxonomic studies were divided into two groups. The first group was treated with vinblastine sulfate prior to fixation and the second was not. The gonad of each snail was prepared on a separate slide. Few snails had active mitotic or meiotic cell divisions. Most tissues not pre-treated with spindle inhibitor were not suitable for cytotaxonomic examination because the chromosomes were not well separated. Therefore, the chromosome numbers presented in this report are only from satisfactorily pre-treated cells in which chromosomes could be observed with accuracy.

A comparison of chromosome numbers between the alpha, beta and gamma races of *Tricula aperta* is shown in Table 1. More detailed information is given in Tables 2-7. Photographs of various cytological activities demonstrated in chronological order in each race are shown in Figs. 1-26. Comparison of karyotypes between the alpha, beta and gamma races are demonstrated in Fig. 27. The details of observations on alpha, beta and gamma snails are as follow.

Tricula aperta, alpha race (Tables 1-3; Figs. 1-13)

Specimens used for chromosomal study were all field collected from a single snail population inhabiting a small pool on the largest rock island in the Mekong River near Ban Khi Lek (see fig. 3, Kitikoon, 1981; fig. 9E, Kitikoon et al., 1981). The pools were connected to each other during the flood period and were isolated in the dry season. However, snails collected from these pools were not different in shell morphology. Therefore, I presumed there is only one population of the alpha snails on this island.

TABLE 1. Comparison of chromosome numbers observed in the three races of *Tricula aperta*.

Race	Haploid numbers observed		Diploid numbers observed	
	Male	Female	Male	Female
Alpha	n = 13-17	n = 16, 17	n = 29, 31, 33	n = 32, 34
Beta	n = 14-17	n = 17	n = 31, 33	n = 34
Gamma	n = 14-17	n = 16, 17	n = 29, 31, 33	n = 32, 34

Meiotic cell divisions were observed from 10 males and three females. The prophase I cells (at late diakinesis) of alpha race males had a greater variation in chromosome numbers than observed in the beta and gamma snails. They were 12 bivalents + 1 trivalent, 13 bivalents + 1 trivalent, 14 bivalents + 1 trivalent and 15 bivalents + 1 trivalent (Table 2; Figs. 9-12). In the females, there were either 16 or 17 bivalents (Table 2). Therefore, the ranges of haploid chromosome numbers were 13 to 17 (Table 1). The modal haploid chromosome numbers in males were 16 or 17 and in females 17.

The mitotic metaphase cells observed from 11 males had 29, 31 and 33 chromosomes, and 23 females had 32 or 34 chromosomes (Tables 1, 3; Figs. 1-4; cells with 29 chromosomes not shown). In males, the two largest pairs and one unmatched chromosome were found to be medially constricted. The remainder were nearly medially, submedially or nearly subterminally constricted chromosomes, and acrocentric chromosomes (Figs. 1, 2, 27a). Three unmatched chromosomes were seen easily when karyotyping was done.

TABLE 2. Chromosome numbers observed in prophase I in individuals of the alpha race of *Tricula aperta*.

Snail	Number of cells observed						
	12 biv. + 1 triv. n=13, 14	13 biv. + 1 triv. n=14, 15	14 biv. + 1 triv. n=15, 16	14 biv. + 1 triv. + 1 univ. n=16, 17	15 biv. + 1 triv. n=16, 17	16 biv. n=16	17 biv. n=17
M 1	0	0	2	0	1	0	0
M 2	1	1	3	0	2	0	0
M 3	0	0	0	0	1	0	0
M 4	0	1	7	0	15	0	0
M 5	0	1	1	0	4	0	0
M 6	3	6	2	0	6	0	0
M 7	0	7	15	0	34	0	0
M 8	0	0	2	0	15	0	0
M 9	0	1	0	0	2	0	0
M 10	0	0	1	0	1	0	0
Total	4	17	33	0	81	0	0
F 1	0	0	0	0	0	1	1
F 2	0	0	0	0	0	0	2
F 3	0	0	0	0	0	0	1
Total	0	0	0	0	0	1	4

Abbreviations: biv. = bivalent; F = female; M = male; triv. = trivalent; univ. = univalent.

Tricula aperta, beta race (Tables 1, 4, 5; Figs. 14-18, 27b)

The snails employed in this study were collected from a single population of the beta race in the Mune River at Kaeng Kao (see C, fig. 11, in Kitikoon et al., 1981). This snail population lived at the bottom of the river and clung to small rocks scattered around the bushy areas in the swift current. The snails were prepared for cytotaxonomic studies in the same manner described previously for the other races of *Tricula aperta*.

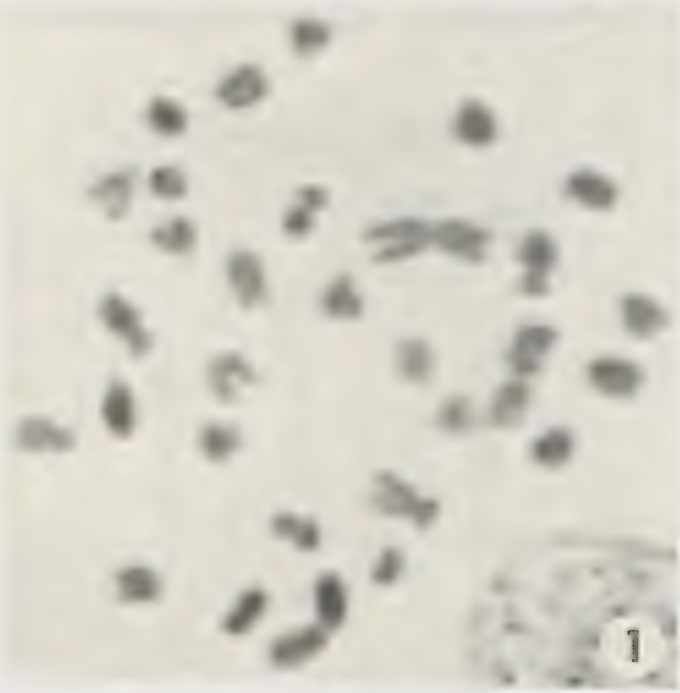
Only nine males and 12 females had satisfactory cell divisions for cytological examination. The prophase I cells (at late diakinesis) of this race had less variation in chromosome numbers than that observed in the alpha population. In four males there were 13 bivalents + 1 trivalent, 14 bivalents + 1 trivalent or 15 bivalents + 1 trivalent (Table 4). In the two females from which observations on prophase I cells were made, the only chromosome configuration found was 17 bivalents (Table 4; Fig. 18). Therefore, the ranges of haploid chromosome numbers were from 14-17.

TABLE 3. Observations on the chromosome numbers of individuals of the alpha race of *Tricula aperta*.

Snail	Number of cells counted					
	2n = 29	2n = 30	2n = 31	2n = 32	2n = 33	2n = 34
M 1	0	0	0	0	1	0
M 2	0	0	0	0	2	0
M 3	0	0	0	0	1	0
M 4	0	0	0	0	1	0
M 5	0	0	5	0	0	0
M 6	0	0	1	0	0	0
M 7	0	0	1	0	1	0
M 8	0	0	1	0	1	0
M 9	0	0	1	0	1	0
M 10	0	0	0	0	1	0
M 11	3	0	0	0	2	0
Total 11 M	3	0	9	0	11	0
F 1	0	0	0	2	0	7
F 2	0	0	0	2	0	1
F 3	0	0	0	0	0	1
F 4	0	0	0	2	0	1
F 5	0	0	0	1	0	2
F 6	0	0	0	0	0	2
F 7	0	0	0	3	0	2
F 8	0	0	0	6	0	6
F 9	0	0	0	0	0	1
F 10	0	0	0	2	0	0
F 11	0	0	0	1	0	0
F 12	0	0	0	1	0	0
F 13	0	0	0	1	0	0
Total 13 F	0	0	0	21	0	23

Abbreviations: F = female; M = male.

The mitotic metaphase cells of males had 31 and 33 chromosomes and females had 34 chromosomes (Tables 1, 5; Fig. 14). In males, the two largest pairs of chromosomes and one unmatched chromosome were found to be medially constricted. The rest were subterminally constricted and acrocentric chromosomes (Fig. 27b).



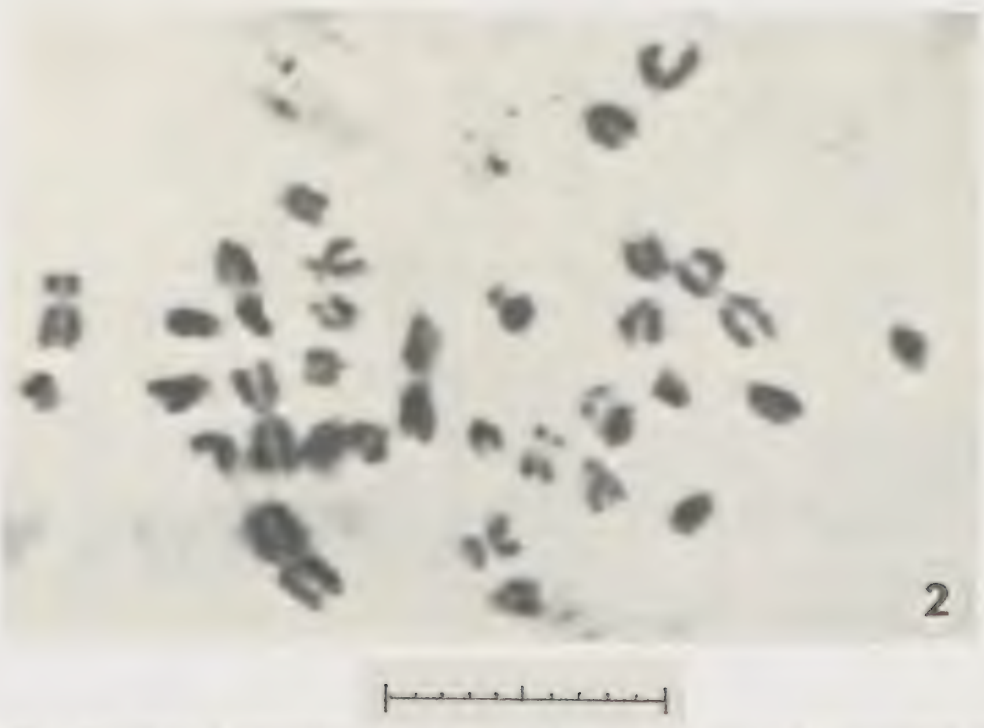


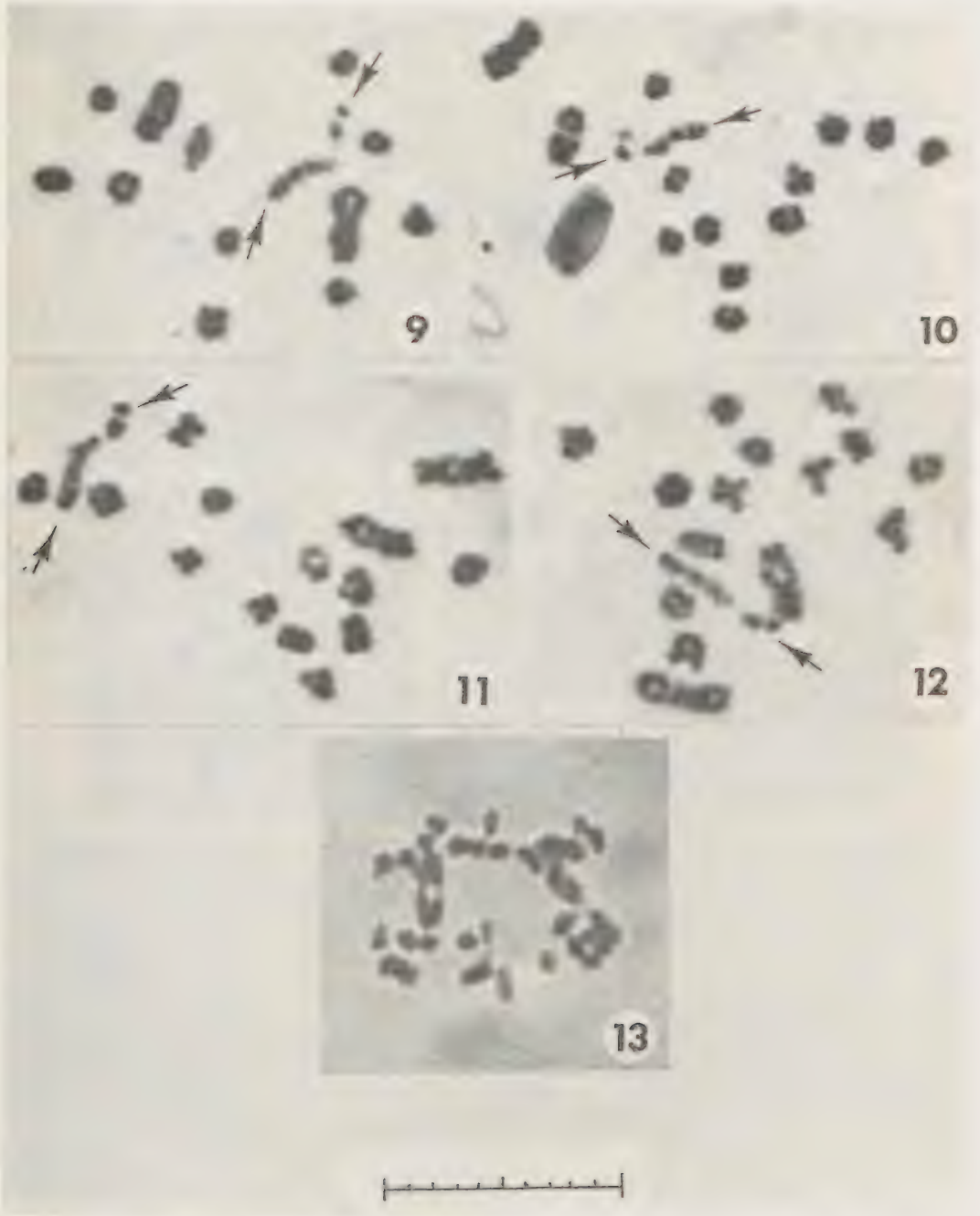
FIG. 1. Photograph of spermatogonial late metaphase chromosomes (2n=31) of *Tricula aperta*, alpha race (one large pair of chromosomes was out of the optical field). FIG. 2. Photograph of spermatogonial late metaphase chromosomes (2n=33) of *T. aperta*, alpha race. The scale is divided into micrometers.

FIG. 3. Photograph of oögonial metaphase chromosomes (2n=32) of the alpha race of *Tricula aperta*.
FIG. 4. Photograph of oögonial metaphase chromosomes (2n=34) of the alpha race of *T. aperta*. The scale is divided into micrometers.

Tricula aperta, gamma race (Tables 1, 6, 7; Figs. 19-26, 27c)

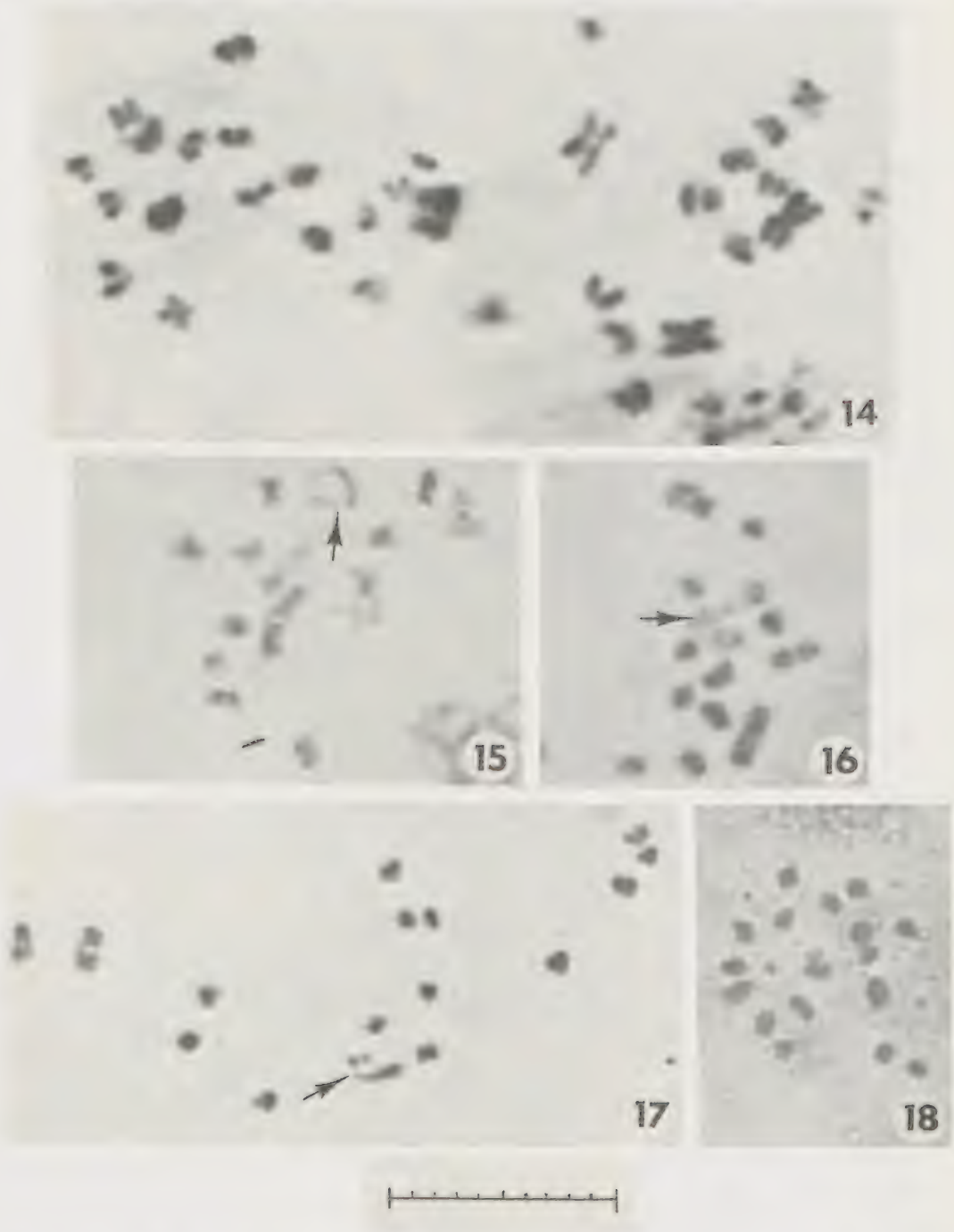
The gamma race of *Tricula aperta* used in this study was field-collected from one population in the Mekong River. This population occurred on the river bottom in front of Ban Bung Kong (see fig. 2, Kitikoon, 1981; fig. 9C, Kitikoon et al., 1981). Like the alpha race, they also clung

FIGS. 5-8. Photographs of various stages of male meiotic cell divisions of *Tricula aperta*, alpha race. FIG. 5. a, Early diplonema; b, late diplonema. FIG. 6. a, Late diplonema or early diakinesis with 15 bivalents and one trivalent (arrows indicate trivalent); b, mid-diakinesis (arrows indicate a trivalent). FIG. 7. Mid-diakinesis. Arrow indicates a trivalent; two arrows indicate closed loop terminalization. FIG. 8. Mid-late diakinesis with 14 bivalents and one trivalent (arrows). Each division of the scale is equal to one micrometer.



FIGS. 9-13. Photographs of stages of division in meiosis I in males of the alpha race of *Tricula aperta*. FIG. 9. Late diakinesis with 12 bivalent and one trivalent (arrows) chromosomes. FIG. 10. Late diakinesis with 13 bivalent and one trivalent (arrows) chromosomes. FIG. 11. Late diakinesis with 14 bivalent and one trivalent (arrows) chromosomes. FIG. 12. Late diakinesis with 15 bivalent and one trivalent (arrows) chromosomes. FIG. 13. Male anaphase I, showing spindle fibers (untreated cell). The scale is divided into micrometers.

to the rocks in the fast current. A few individuals of the alpha race of *T. aperta* were found with these gamma snails, but apparently the maturation of gametes in the latter occurred at different times. Hybrids between the two races have never been found in nature, and cross-breeding in the laboratory has not been attempted because of the difficulty in culturing these



FIGS. 14-18. Photographs of various stages of cell division in males and females of the beta race of *Tricula aperta*. FIG. 14. Spermatogonial metaphase chromosomes (2n=33). FIG. 15. Late male diakinesis with 13 bivalent and one trivalent (arrow) chromosomes. FIG. 16. Late male diakinesis with 14 bivalent and one trivalent (arrow) chromosomes. FIG. 17. Late male diakinesis with 15 bivalent and one trivalent (arrow) chromosomes. FIG. 18. Late female diakinesis with only 17 bivalents. The scale is divided into micrometers.

TABLE 4. Chromosome numbers observed in prophase I of individuals of the beta race of *Tricula aperta*.

Snail	Number of cells observed						
	12 biv. + 1 triv. n=13, 14	13 biv. + 1 triv. n=14, 15	14 biv. + 1 triv. n=15, 16	14 biv. + 1 triv. + 1 univ. n=16, 17	15 biv. + 1 triv. n=16, 17	16 biv. n=16	17 biv. n=17
M 1	0	0	1	0	3	0	0
M 2	0	0	0	0	1	0	0
M 3	0	1	6	0	9	0	0
M 4	0	0	6	0	6	0	0
Total	0	1	13	0	19	0	0
F 1	0	0	0	0	0	0	6
F 2	0	0	0	0	0	0	5
Total	0	0	0	0	0	0	11

Abbreviations: biv. = bivalent; F = female; M = male; triv. = trivalent; univ. = univalent.

snails. Therefore, I assumed that all gamma race specimens of *T. aperta* that I used for my studies came from a single population and were not hybrids.

Observations on the chromosome numbers at various stages of cell division were made from 18 males and 12 females. The variations of prophase I chromosomes in males were 13 bivalents + 1 trivalent, 14 bivalents + 1 trivalent, 14 bivalents + 1 trivalent + 1 univalent and 15 bivalents + 1 trivalent (Table 6; Figs. 22-25). Females had 16 or 17 bivalents (Table 6). The ranges of haploid chromosome numbers were 14-17 in males and 16 and 17 in females (Table 1).

The diploid chromosome numbers were observed in late metaphase and early anaphase of spermatogonial or oõgonial cells. There were 29, 31 and 33 chromosomes in males and 32 or 34 chromosomes in females (Tables 1, 7; Figs. 19-21). The karyotypes are illustrated in Fig. 27c. The two largest pairs and one unmatched chromosome are also medially constricted, and the remainder are subterminally or nearly subterminally constricted chromosomes (Fig. 27c). The three unmatched chromosomes were also seen in the gamma snails. Various stages of spermatogenesis are demonstrated in Fig. 26.

Karyotypes (Fig. 27)

The karyotypes were determined from male mitotic metaphase cells having 31 chromosomes. The chromosome configurations were made directly from photographs of single cells, taking great care to compare them to the chromosomes of the other cells in the same race prior to karyotyping. The chromosomes compared during the course of these studies were from photographs of the same magnification. The results of the observations follow.

The gonial metaphase karyotype of the alpha race of *Tricula aperta* (Fig. 27a) comprises (a) two pairs of medially constricted chromosomes with long arms (chromosome pairs 1 and

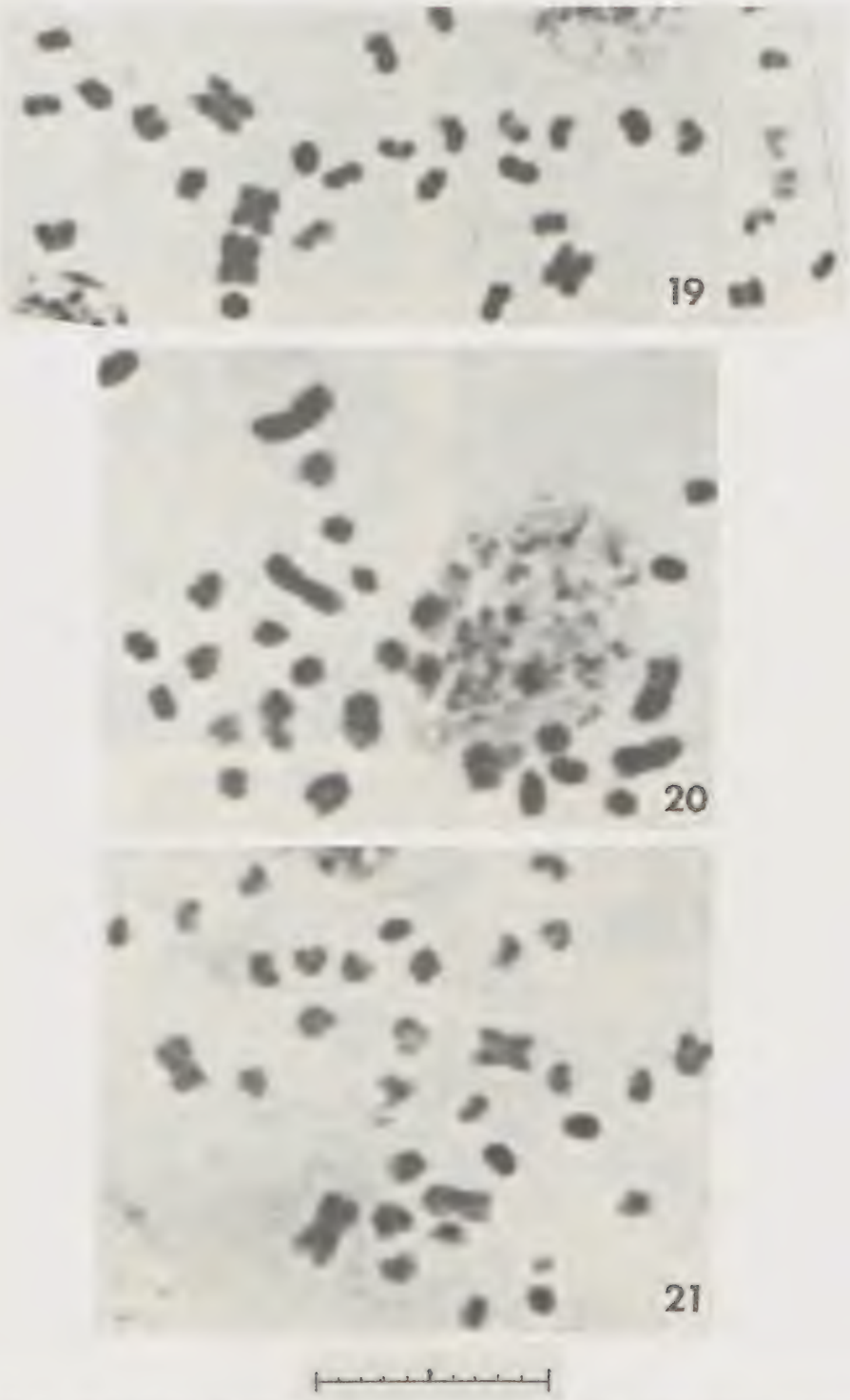
TABLE 5. Chromosome numbers observed in individuals of the beta race of *Tricula aperta*.

Snail	Number of cells counted					
	2n = 29	2n = 30	2n = 31	2n = 32	2n = 33	2n = 34
M 1	0	0	1	0	0	0
M 2	0	0	6	0	5	0
M 3	0	0	2	0	7	0
M 4	0	0	1	0	0	0
M 5	0	0	0	0	3	0
M 6	0	0	0	0	3	0
M 7	0	0	1	0	4	0
M 8	0	0	0	0	2	0
M 9	0	0	1	0	0	0
Total 9 M	0	0	12	0	24	0
F 1	0	0	0	0	0	2
F 2	0	0	0	0	0	2
F 3	0	0	0	0	0	2
F 4	0	0	0	0	0	6
F 5	0	0	0	0	0	3
F 6	0	0	0	0	0	8
F 7	0	0	0	0	0	3
F 8	0	0	0	0	0	2
F 9	0	0	0	0	0	4
F 10	0	0	0	0	0	10
F 11	0	0	0	0	0	1
F 12	0	0	0	0	0	1
Total 12 F	0	0	0	0	0	44

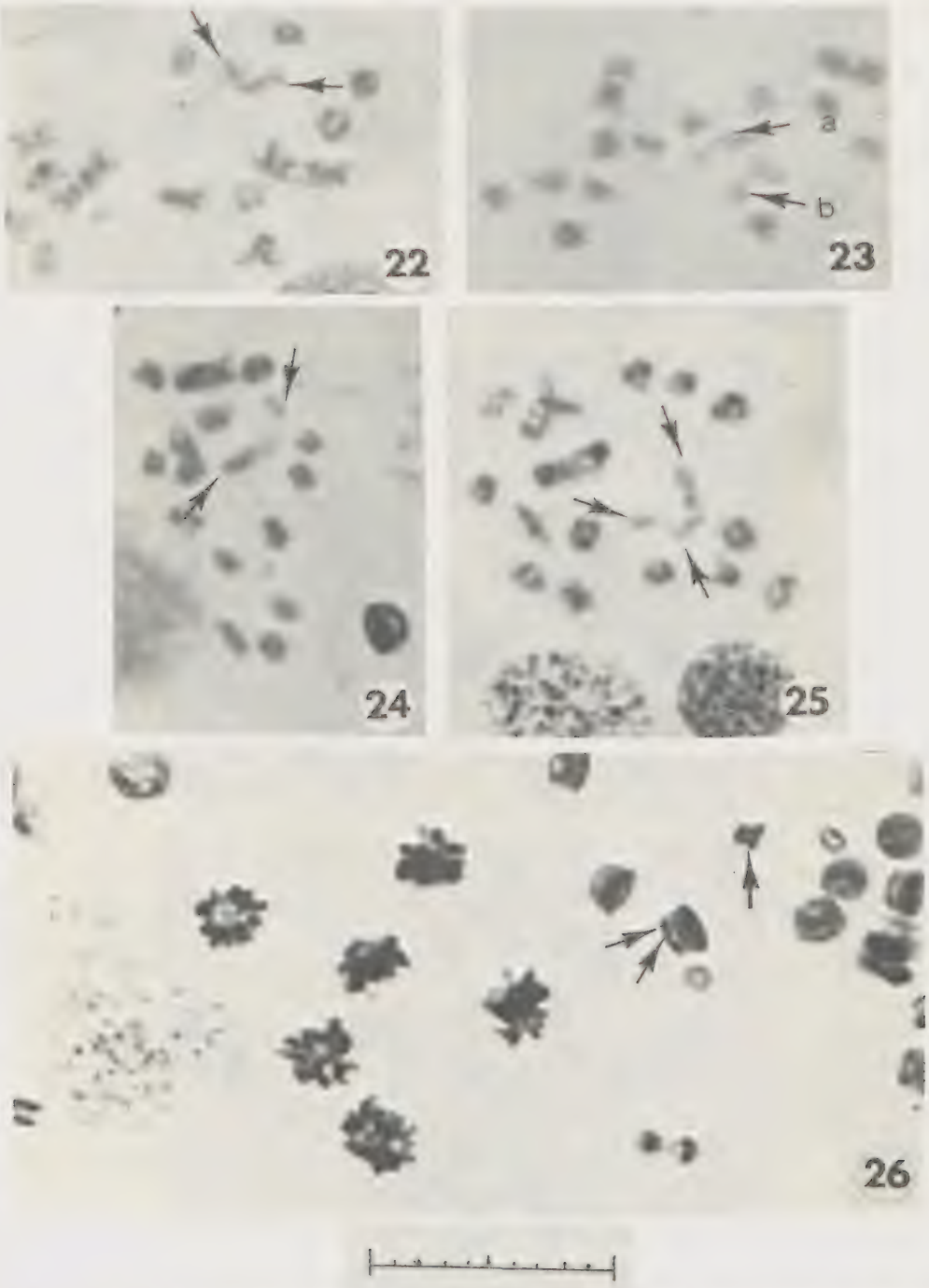
Abbreviations: F = female; M = male.

2), (b) two pairs of nearly medially constricted chromosomes (chromosome pairs 3 and 4), (c) two pairs of submedially or nearly submedially constricted chromosomes (chromosome pairs 5 and 6), (d) eight pairs of subterminally or nearly subterminally constricted chromosomes with long arms (chromosome pairs 7-12) and short arms (chromosome pairs 13 and 14), (e) one pair of acrocentric chromosomes (chromosome pair 15) and (f) three odd chromosomes, one of which is submetacentric (chromosome 31), one is metacentric (chromosome 32), and one is acrocentric (chromosome 33).

The gonial metaphase karyotype of the beta race of *Tricula aperta* (Fig. 27b) is composed of (a) nine pairs of medially constricted chromosomes with long arms (chromosome pairs 1



FIGS. 19-21. Photographs of mitotic cell division in males and females of the gamma race of *Tricula aperta*. FIG. 19. Spermatogonial metaphase chromosomes (2n=33). FIG. 20. Oögonial metaphase chromosomes (2n=32). FIG. 21. Oögonial metaphase chromosomes (2n=34). The scale is divided into micrometers.



FIGS. 22-26. Photographs of various stages of meiotic cell division in males of the gamma race of *Tricula aperta*. FIG. 22. Late diakinesis with 13 bivalent and one trivalent (arrows) chromosomes. FIG. 23. Late diakinesis with 14 bivalent and one trivalent (arrow a) plus one univalent (arrow b) chromosomes. FIG. 24. Late diakinesis with 14 bivalent and one trivalent (arrows) chromosomes. FIG. 25. Late diakinesis with 15 bivalent and one trivalent (arrows) chromosomes. FIG. 26. Various stages of spermatogenesis; an arrow indicates head of mature spermatozoa; two arrows (pointed together) indicate a spermatid. The scale is divided into micrometers.

TABLE 6. Chromosome numbers observed in prophase I in individuals of the gamma race of *Tricula aperta*.

Snail	Number of cells observed						
	12 biv. + 1 triv. n=13, 14	13 biv. + 1 triv. n=14, 15	14 biv. + 1 triv. n=15, 16	14 biv. + 1 triv. + 1 univ. n=16, 17	15 biv. + 1 triv. n=16, 17	16 biv. n=16	17 biv. n=17
M 1	0	0	1	0	13	0	0
M 2	0	0	0	4	4	0	0
M 3	0	0	0	0	1	0	0
M 4	0	0	3	1	4	0	0
M 5	0	0	0	1	0	0	0
M 6	0	0	1	0	1	0	0
M 7	0	0	1	1	1	0	0
M 8	0	0	1	0	1	0	0
M 9	0	0	1	0	2	0	0
M 10	0	2	0	0	4	0	0
M 11	0	0	2	0	3	0	0
Total	0	2	10	7	34	0	0
F 1	0	0	0	0	0	2	0
F 2	0	0	0	0	0	1	4
F 3	0	0	0	0	0	0	2
Total	0	0	0	0	0	3	6

Abbreviations: biv. = bivalent; F = female; M = male; triv. = trivalent; univ. = univalent.

and 2) and short arms (pairs 3-9), (b) one pair of submedially constricted chromosomes (pair 10), (c) two pairs of subterminally constricted chromosomes (pairs 11 and 12), (d) three pairs of acrocentric chromosomes (pairs 13-15), and (e) three unmatched chromosomes, one of which is submedially constricted (chromosome 31), one is medially constricted (chromosome 32) and one is acrocentric (chromosome 33).

The gonial metaphase karyotype of the gamma race of *Tricula aperta* (Fig. 27c) consists of (a) nine pairs of metacentric chromosomes with long arms (chromosome pairs 1 and 2) and short arms (pairs 3-9), (b) one pair of submetacentric chromosomes (pair 10), (c) three pairs of subterminally or nearly subterminally constricted chromosomes (pairs 11-13), (d) two pairs of acrocentric chromosomes (pairs 14 and 15), and (e) three unmatched chromosomes, one of which is subterminally constricted (chromosome 31), one is metacentric (chromosome 32) and one is acrocentric (chromosome 33).

Many cells in the males of all three races were found to have fewer than 31 chromosomes (Tables 1, 3, 5, 7). This was carefully investigated. The absent chromosomes in the alpha

TABLE 7. Number of chromosomes counted in individuals of the gamma race of *Tricula aperta*.

Snail	Number of cells counted					
	2n = 29	2n = 30	2n = 31	2n = 32	2n = 33	2n = 34
M 1	0	0	0	0	2	0
M 2	1	0	1	0	0	0
M 3	0	0	1	0	0	0
M 4	0	0	2	0	0	0
M 5	0	0	0	0	1	0
M 6	0	0	1	0	0	0
M 7	0	0	0	0	1	0
M 8	0	0	0	0	1	0
M 9	0	0	1	0	0	0
M 10	0	0	0	0	1	0
M 11	0	0	0	0	2	0
M 12	0	0	2	0	3	0
M 13	0	0	0	0	2	0
M 14	0	0	0	0	1	0
M 15	3	0	0	0	1	0
M 16	1	0	4	0	6	0
M 17	0	0	4	0	1	0
Total 17 M	5	0	16	0	22	0
F 1	0	0	0	3	0	0
F 2	0	0	0	0	0	1
F 3	0	0	0	0	0	1
F 4	0	0	0	2	0	0
F 5	0	0	0	2	0	0
F 6	0	0	0	1	0	2
F 7	0	0	0	0	0	1
F 8	0	0	0	0	0	4
F 9	0	0	0	1	0	0
F 10	0	0	0	0	0	1
F 11	0	0	0	0	0	3
F 12	0	0	0	0	0	1
Total 12 F	0	0	0	9	0	14

Abbreviations: F = female; M = male.

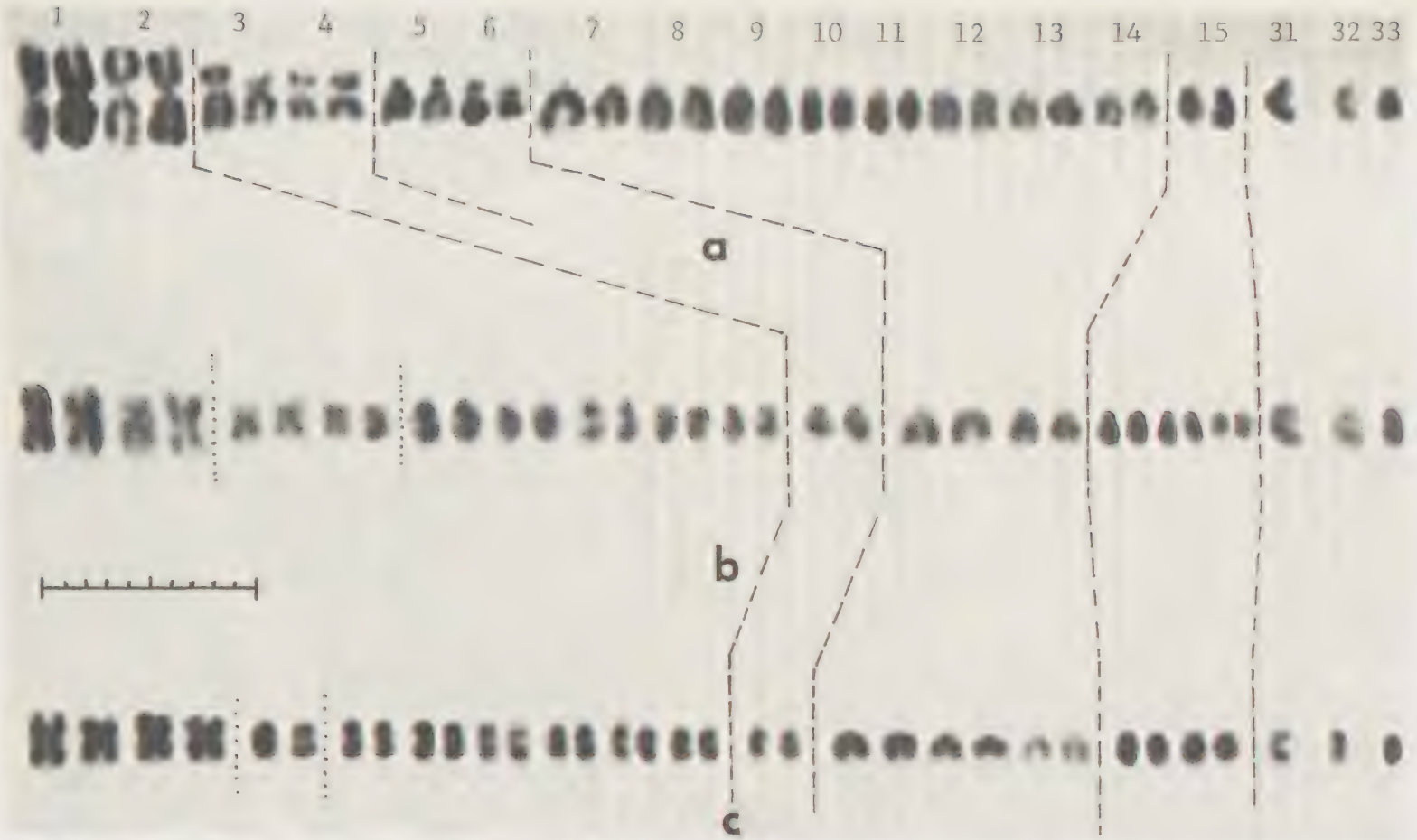


FIG. 27. Comparison of the karyotypes of the three races of *Tricula aperta*, using male mitotic late metaphase chromosomes aligned according to shapes and sizes. The vertical interrupted lines separate chromosome types. Three odd chromosomes in each race are aligned on the far right. This may form a trivalent in early meiotic prophase I. The chromosome configurations in each race were made from a photograph of a single cell having 33 chromosomes, carefully compared with others prior to karyotyping. The scale is divided into micrometers. Morphological details are presented in the text. a, *T. aperta*, alpha race; b, *T. aperta*, beta race; c, *T. aperta*, gamma race.

race of *Tricula aperta* were pairs 12 or 13 or both pairs. In the beta race, the absent chromosomes comprised a pair with short arms (one of the pairs 3-9, but just which one was difficult to determine precisely). In the gamma race, the absent chromosomes occurred in two groups. Some short arm chromosomes of pairs 3-9 (just which pair was hard to identify) or the 13th pair were normally absent. The three unmatched chromosomes might give rise to a trivalent during early prophase I cell division. (In females there were no satisfactory cells available for karyotyping.)

Comparative observations on the various morphological groups of mitotic metaphase chromosomes among the three races are given below. They show some interesting contrasts.

The metacentric or medially constricted chromosome group. The alpha race of *Tricula aperta* had only two pairs of metacentric chromosomes (pairs 1 and 2). These all had long arms. The beta race had nine pairs of metacentric chromosomes, two of which had long arms (pairs 1 and 2) and seven of which had short arms that could be divided into two smaller groups: a group of five pairs with medium-sized arms (pairs 3-7, as compared to the long arms) and two pairs with small arms (pairs 8 and 9, as compared to the medium-sized arms). Also, the arms of the chromosomes in the first two pairs with the medium-sized arms (pairs 3 and 4) were very well separated, which might have resulted from the pressure of the squash procedure, or may have been due to the nature of the chromosomes. There were nine pairs of metacentrically constricted chromosomes in the gamma race. The first two pairs (pairs 1 and 2) were long-armed chromosomes, and the last seven pairs (pairs 3-9) were short-armed chromosomes, which appeared to be the same number of pairs present in the beta race. However, the differences in morphological features of the chromosomes between the latter two races easily could be seen. All short-armed chromosomes of the gamma race were undoubtedly more or less equal in size, but that was not the case in the beta race, as described previously. However, it should be pointed out here that, due to the difficulty of karyotyping, the chromosome pairs 5-9 of the beta race and pairs 4-9 in the gamma race might belong to either subterminally or to nearly subterminally constricted groups of the respective races. Nevertheless, whichever way the two groups are interpreted will not change the differences between the beta and gamma races in terms of the number of chromosome pairs.

The nearly metacentric or nearly medially constricted chromosome group. Two pairs of chromosomes (pairs 3 and 4) in the alpha race exhibited nearly metacentric constrictions. These chromosomes seemed to be equal in size, except for one chromosome of the third pair. This one appeared to be larger when compared to the other chromosomes in the same group. This possibly may have been due to the physical alignment caused by the pressure of the squash or to differences in focal alignment of individual chromosomes when the photographs were taken. None of the chromosomes in the beta race were nearly metacentric, and only one pair of chromosomes (pair 10) in the gamma race was nearly metacentric. Undoubtedly, the three so-called "races" of *Tricula aperta* are distinctly different in regard to the number of nearly metacentric chromosomes.

The submetacentric or submedially constricted chromosome group. Two pairs of submedially constricted chromosomes (pairs 5 and 6) could be counted in the alpha race. They were more or less of the same size, except that one chromosome of the sixth pair looked smaller in size, which was due to its position when the photograph was taken. Only one pair of submetacentric chromosomes (pair 10) was found in the beta race and none were found in the gamma race. It is obvious that the three races, alpha, beta and gamma, are different in regard to submetacentrically constricted chromosomes.

The subterminally constricted (subtelocentric) or nearly subterminally constricted (nearly subtelocentric) chromosome group. There were larger numbers of pairs of subterminally constricted chromosomes in the alpha race (pairs 7-14) than in the other two races. The definite number of subterminally constricted pairs on the beta race was two (pairs 11 and

12), but it possibly could be increased to seven pairs if pairs 5-9 were to be included as subterminally constricted chromosomes, as mentioned previously. Actually, the size of the chromosomes of pair 12 was smaller than those of pair 11. But, it is too risky to compare the sizes of the chromosomes in pairs 11 and 12 with those of pairs 5-9, since the nature of their alignments was not the same. However, the chromosomes of pairs 5-7 were larger than those of pairs 8 and 9. The same situation occurred in the gamma race, where the definite number of subterminally constricted chromosomes was three pairs. But, the number possibly could be nine pairs, if pairs 4-9 were counted as subtelocentric as stated previously. The chromosomes of pairs 4-9 appeared to be the same in size, as mentioned formerly, and it was impossible to compare them with those of the 11th, 12th and the 13th pairs. Obviously, the size of the chromosomes of pair 11 was larger than those of pairs 12 and 13. However, no matter how the chromosomes may be rearranged, the differences among the number of pairs and the morphological features of the chromosomes in this subtelocentric group will still exist between the three races.

The acrocentric chromosome group. There were one pair (pair 15), three pairs (13-15) and two pairs (14 and 15) of acrocentric chromosomes in the alpha, beta and gamma snails, respectively, The acrocentric chromosomes of the alpha race were intermediate in size between the small and the medium-sized chromosomes, and one was deeply stained. In the beta race, two pairs of chromosomes were large (pairs 13 and 14) and one pair (15) was comparatively small. Further, the degree of staining seemed to be different among the three pairs. Pair 13 was very deeply stained, while pair 14 was intermediate and pair 15 was very lightly stained. The sizes of the acrocentric chromosomes in the gamma race were relatively the same, and they were all very deeply stained.

Unmatched chromosomes. The three unmatched chromosomes were found to be the same in all three races of *Tricula aperta* – one was submedially constricted (chromosome 31), one was metacentric (chromosome 32) and one was acrocentric (chromosome 33).

DISCUSSION

These studies show that there is some variation in chromosome numbers within and between the races of *Tricula aperta*. The haploid number in the male alpha snails ranged from 13-17, whereas it ranged from 14-17 in the beta and gamma snails (Table 1). Moreover, 14 bivalents + 1 trivalent + 1 univalent easily could be seen in some individuals (four out of 11) of the gamma race, while this pairing combination of the chromosomes was not found in the other two races. Although trivalents and univalents occurred in the males, only bivalents were observed in the females of all three races (Tables 2, 4, 6). In females, there was no variation in haploid number in the beta race (n=17), whereas the other two races had individuals with n=16 or n=17 (Table 1). The diploid chromosome number also showed some degree of variation. Males of the beta race had 2n=31 and 33, whereas males of the alpha and gamma races had 2n=29, 31 and 33. Females of the alpha and gamma races had 2n=32 and 34, while the beta females had 2n=34 chromosomes (Table 1).

Variation in chromosome numbers of individuals in populations of streptoneuran snails has been occasionally reported, especially in the Mesogastropoda. For example, Pollister & Pollister (1940) reported that *Campeloma decisum* and *C. subsolidum* of the family Viviparidae both have n=13 or n=14 chromosomes. Later, Jacob (1959) reported that the polyploid chromosome numbers of the thiarid *Melanoides tuberculatus* was n=45-47, *M. (Tarebia) lineatus* was n=35-36, and *Thiara scabra* was n=38-39 chromosomes. However, apparent variation in numbers may have been an artifact of the methods he used (paraffin sectioning). More recently, Burch (1968) observed chromosomal number variations in Japanese freshwater snails of the family Pleuroceridae. For example, *Semisulcospira multigranosa* had 2n=28-31

chromosomes, and he inferred that its basic haploid number was n=14. He also reported that other species of *Semisulcospira*, i.e., *S. kurodai, S. niponica, S. decipiens, S. reticulata* and *S.* sp. (*S. habei*) had some degree of variation in chromosome numbers within species. The chromosome numbers of 2n + 1 were commonly seen in both sexes in the Japanese snails, whereas, in my observations on *Tricula*, the 2n + 1 chromosomes appeared only in male snails and the females had even chromosome numbers. Therefore, it would appear from my observations that the extra chromosome in males in all three races may be related to sex determination. Thus, the males would have basically an XO chromosome sex-determining mechanism and the females would have XX. This needs to be confirmed.

The subfamily Triculinae is quite small and formerly had little known medical and veterinary importance in comparison to the related subfamily Pomatiopsinae. A cytotaxonomic study of *Tricula* species had not been made previously. Therefore, there is no other information on triculine snails with which to compare my cytological studies on the three races of *T. aperta*. There are, however, several reports on the closely related subfamily Pomatiopsinae, i.e., snails of the genera *Oncomelania* and *Pomatiopsis*. Burch (1960, 1964) reported that four subspecies (geographic races) of *Oncomelania hupensis*, i.e., *O. h. hupensis* (mainland China), *O. h. nosophora* (Japan), *O. h. quadrasi* (Philippines) and *O. h. formosana* (Formosa), and their F_1 hybrids have the same haploid chromosome numbers, n=17. He also found that a difference in diploid chromosome numbers exists between male *Pomatiopsis lapidaria* (2n=33) and *P. cincinnatiensis* (2n=32). Burch did not report any variations in chromosome numbers within populations of these snails.

Changes in chromosome numbers in animals may occur by (a) chromosomal fusion; (b) fragmentation; (c) meiotic or mitotic non-disjunction; (d) translocations involving a supernumerary fragment serving as a donor of a centromere and two telomeres; and (e) duplication of entire chromosomal complements through polyploidy (Patterson & Burch, 1978). Chromosomal fusion results in a decrease in chromosome number, whereas the other mechanisms produce an increase in chromosome number. Most variation in chromosome numbers of mollusks within a taxon is seldom greater than ± 1 or 2 bivalents, and in many taxa all species have the same chromosome number. Therefore, mechanisms for addition or deletion of chromosomes must operate at a low or inefficient level (Burch, 1965; Patterson, 1969). Nearly all changes in chromosome numbers that occurred which are now evident undoubtedly represent aneuploid conditions which became stabilized. Husted & P.R. Burch (1946) pointed out that diploid species can tolerate duplications or additions of chromosomes more easily than loss of chromosomes. Thus, variation in chromosome numbers within a taxon probably usually reflects addition rather than loss of chromosomes.

Burch (1968) followed this hypothesis by giving the lowest number in the range of chromosomal variation as the basic chromosome number for *Semisulcospira*, i.e., n=14 for *S. multigranosa*, n=14 for *S. kurodai*, n=12 for *S. niponica*, n=12 for *S. decipiens*, n=12 for *S. reticulata* and n=7 for *S.* sp. (=*S. habei*), etc. Applying this reasoning to my results, the basic chromosome number of the alpha race of *Tricula aperta* would be n=13, and for the beta and gamma races it would be n=14. Supporting the lower basic chromosome number of the alpha race is the low pairing configuration of 12 bivalents + 1 trivalent seen only in that race.

A comparison of karyotypes obtained from spermatogonial mitotic metaphase chromosomes of the alpha, beta and gamma races shows distinct differences in morphology of chromosomes between the three races. These differences fall into three categories: (a) number of different centromeric groups; (b) number(s) of homologous pairs of chromosomes in each centromeric group; and (c) number of homologous pair(s) of chromosomes within each centromeric group in each race having morphological size differences.

Since the centromeric region of any chromosome is generally fixed, centromeric positions may be important for indicating species differences. With this in mind, it is interesting to

compare the three races of *Tricula aperta*. In the alpha race, five sets of chromosomes may be distinguished by their centromeric positions (Fig. 27a). These sets are metacentric, nearly metacentric, submetacentric, subtelocentric or nearly subtelocentric and acrocentric chromosomes. In the beta (Fig. 27b) and the gamma races (Fig. 27c), four morphological types of chromosomes appear to be the same as in the alpha race; the set excluded from the beta and gamma races, but present in the alpha race, is a group of nearly metacentric chromosomes.

Burch (1968) showed that *Semisulcospira reticulata* differed from other members of the genus by having only acrocentric chromosomes and concluded that this difference represented a very good species-differentiating character, indicating *S. reticulata*'s distinctness from the other species of the genus. Further, *S. nakasekoae* had its own distinct characteristic karyotype, as did *S. decipiens* and *S. niponica*. (Although the latter two species could not be distinguished from each other by their karyotypes, other characteristics easily separated them.) Similarly, the distinctness of the karyotype of the alpha race of *Tricula aperta* from the other two races would seem to be good evidence that the alpha race is really a cytologically distinct species.

Chromosome complements, as defined by both the number and individual morphology of mitotic metaphase chromosomes, are usually different among the various animal and plant species. Therefore, the number of homologous pairs and the size of individual chromosomes within the centromeric groups lend important support to species delineation. The results of my comparative observations on the karyotypes of the three races of *Tricula aperta* show various differences in numbers and sizes of individual pairs of chromosomes within the various centromeric groups (Fig. 27).

Therefore, I conclude that the alpha, beta and gamma snails represent at least distinct races, and possibly (? probably) they may be different species.

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STUDIES ON *TRICULA APERTA* AND RELATED TAXA, THE SNAIL INTERMEDIATE HOSTS OF *SCHISTOSOMA MEKONGI*. V. ELECTROPHORETIC STUDIES

Viroj Kitikoon

ABSTRACT

Allozymes of the alpha, beta and gamma races of *Tricula aperta* were analyzed using horizontal starch gel electrophoresis. Twelve selected enzymatic activities were studied: acid phosphatase, alanine aminopeptidase, alkaline phosphatase, non-specific esterases, glutamate oxaloacetate transaminase, leucine aminopeptidase, maleate dehydrogenase, octanol dehydrogenase, sorbital dehydrogenase, α-glycerophosphate dehydrogenase, β-hydroxybutyrate dehydrogenase and xanthine oxidase. Genotypic differences between the three races were observed in the electrophoretically separated isozymes alkaline phosphatase, various esterases and glutamate oxaloacetate transaminase. The differences in susceptibilities of the three races to schistosome infection possibly may be related to the differences in glutamate oxaloacetate transaminase activity. Allozyme differences between the three races illustrate the distinctiveness of each of the three races, and may be supportive evidence indicating that there is even wider taxonomic separation of the three forms than merely "races".

INTRODUCTION

Electrophoresis first was used in the Mollusca to study land snail blood plasma in 1949 by Deutch & McShan. Later, Wood et al. (1958) utilized starch-gel electrophoresis to study blood proteins of invertebrates, including mollusks. The latter authors suggested that electrophoresis of serum proteins might be very useful for taxonomic studies. Subsequently, electrophoretic studies have been used widely in molluscan systematics by various authors, e.g., Wright & Ross (1963, 1965, 1966), Davis (1967), Davis & Lindsay (1967), Burch & Lindsay (1968), Wu & Burch (1975) and Wurzinger (1979). Details of electrophoresis as used in molluscan systematics were summarized by Davis (1978).

Prior to my present research, electrophoretic studies had never been done on the alpha, beta and gamma races of *Tricula aperta* (Temcharoen). Therefore, I felt that a study of various enzymatic activities, as detected by horizontal starch gel electrophoresis, might yield fruitful information regarding the snails' systematic relationships.

MATERIALS AND METHODS

Snails

The snail populations utilized in the electrophoretic studies were all field-collected in May 1979 from three locations described previously (sites 3, 4 and 7: Kitikoon, 1981a, figs. 2, 3; Kitikoon et al., 1981, figs. 9C, 9E, 11C). Voucher specimens have been deposited in the Applied Malacology Centre, Faculty of Tropical Medicine, Mahidol University, Bangkok. The snails were kept in the laboratory of the Faculty of Tropical Medicine, Mahidol University, for two weeks for acclimatization prior to transporting them to the laboratory in The University of Michigan. These snails were maintained in the latter laboratory for about five months to allow them to grow before they were used in the experiments. They were raised on a mud substrate and fed diatoms (see Kitikoon, 1981a). Prior to enzyme analyses, the snails of each race were divided into two groups and placed in Petri dishes, where they were starved for 48 hr to clear their digestive tracts. The first group contained both sexes, presumably in equal numbers. The second group was separated into male and female groups. All groups were then frozen and stored at -90°C.

Sample preparations

Animals were pooled in the various experiments because the snail samples from each population of the alpha, beta and gamma races of *Tricula aperta* used for my study were not unlimited, they were relatively small in size, and tools and chemicals used were restricted to those which could be obtained within the budget and time available to me. Pooled samples of one sex alone and pooled samples of both sexes were used for enzyme analyses with horizontal starch-gel electrophoresis. The sample preparation procedures are given below.

The snails' shells, resting on ice, were gently cracked while being viewed with a stereo-microscope. Broken pieces of shell were removed with fine dissecting forceps, and the shell-less bodies were ground with a glass pestle in a small glass mortar containing water chilled to 4°C. Prior to use, the pestle and mortar were placed in a deep freeze for about 30 min. Grinding of tissues was aided by small pieces of shell remaining with soft bodies. After being ground, the tissues were placed in Sorvall[R] centrifuge tubes and centrifuged at 16,000 rpm for 30 min at 4°C in a Sorvall RC-2B refrigerated centrifuge equipped with an SS-34 rotor. The clear supernate was then withdrawn using a graduated fixed volume micropipette and stored at -90°C in 50 μl aliquots until used for horizontal starch-gel electrophoresis. Most sets of samples used during electrophoretic studies on each horizontal gel consisted of three different pooled samples prepared from each snail population, with two replications for each sample. Each replicated sample was prepared from a different lot of snails of the same race. Then, 18 different samples were examined on each sample gel in order to detect the presence of any major variants between or possibly within the three populations.

Approximate total weights of animals of the alpha, beta and gamma races of *Tricula aperta* used during the electrophoretic studies were 100 mg, 80 mg and 40 mg per snail, respectively. The average wet weight of the soft tissues in the three races in each case was about one-fifth of their total weight. Therefore, the enzyme samples prepared from 40, 50 and 100 snails of the alpha, beta and gamma races, respectively, using 100 μl of glass-distilled water as a diluent medium, yielded about 5-7 μg of extract per μl.

Horizontal starch-gel electrophoresis

The method used was basically that of Smithies (1959a,b), Smith (1968) and Brewer (1970), with minor modifications.

The samples used for electrophoretic studies were applied to 9 x 5 mm chromatography paper and inserted into a slot cut 3 cm from the cathode end of the starch gel. About 16.5 μl from two different lots of each sample were used on the same gel. From the three snail populations used during the study, three different types of samples were prepared as described previously: pooled male and female, presumably in equal sex ratio; pooled male only; pooled female only.

Following electrophoresis, the gel was sliced horizontally into five 2-mm thick slices using a Buchler-type gel slicer. Each sliced gel was then transferred singly into a staining dish for a specific enzymatic activity stain. The staining was done as soon as possible after slicing, unless stated otherwise. Most of the visualization of enzymatic activities took place within about 20 min in an incubator. Incubation was done in complete darkness to avoid any undesirable effects of light on the stain. However, in some cases, a particular stain took a shorter time and the reaction occurred very quickly. Therefore, in order to get the best banding intensity prior to completion of the reaction, a series of photographs was taken at about 10 sec intervals or less. The stained gel was fixed by simply discarding the staining solution and rinsing once with tap water and adding 10% acid alcohol (10% acetic acid, 50% ethanol and 40% water by volume).

Starch-gel electrophoresis buffers

Four different buffer systems were used to detect various enzymatic activities. These buffers were buffer system I, the discontinuous buffer system of Poulik (1957); buffer system II, the discontinuous Tris-citrate/lithium hydroxide-borate system of Ashton & Braden (1961); buffer system III, the continuous Tris-EDTA-borate system; buffer system IV, Tris-EDTA-maleate system at pH 7.4 (Spencer et al., 1964).

Electrophoresis was terminated after the bromphenol blue marker dye had migrated 8 cm from the origin. It took about 6 hr at 25 mA/gel for buffer systems I and II, 8 hr at 45 mA/gel for buffer system III and 18 hr at 30 mA/gel for buffer system IV. Due to the limit of sample quantities, not all enzymatic activities were assayed on all four buffer systems. The buffer systems used most routinely were I and II.

Enzyme assays

The snails available for this study were limited, and the number of enzymatic tests had to be restricted to those which could be done within the budget and time available. Therefore, only 12 enzymes were tested. The assay solutions used for detecting these enzymes followed Coles (1969a,b), Shaw & Prasad (1970), Selander et al. (1971) or Wurzinger (1979), with some minor modifications. The enzymatic activities tested and assay solutions were: alanine aminopeptidase (AAP), buffer system I; acid phosphatase (AcP), buffer systems I and II; alkaline phosphatase (AlP), buffer systems I and II; esterase (EST), buffer

systems I and II (the substrates used were α-naphthyl acetate, α-naphthyl proprionate and β-naphthyl acetate); glutamate oxaloacetate transaminase (GOT), buffer systems I, II, III and IV; leucine aminopeptidase (LAP), buffer systems I and II; malate dehydrogenase (MDH), buffer systems I, II, III and IV; octanol dehydrogenase (ODH), buffer systems I, II, III and IV; sorbitol dehydrogenase (SoDH), buffer systems I, II, III and IV; xanthine oxidase (XO), buffer systems I, II, III and IV; α-glycerophosphate dehydrogenase (αGPDH), buffer systems I and II; β-hydroxybutyrate dehydrogenase (βHBDH), buffer systems I and II.

RESULTS

Results of 12 selected enzymatic activities studies using four different buffer systems are shown in Table 1. These selected enzymatic activities were AAP, AcP, AlP, EST (with three different substrates: α-naphthyl acetate, α-naphthyl proprionate and β-naphthyl acetate), GOT, LAP, MDH, SoDH, XO, αGPDH and βHBDH. Buffer systems I and II were used for all of the enzyme tests; buffer systems III and IV were used only for some tests. The use of α-naphthyl acetate and β-naphthyl acetate as the substrates to resolve for non-specific esterase activities was more appropriate than treating with α-naphthyl proprionate in both buffer systems I and II. Only buffer systems I and II were found to be excellent in testing for AAP, AlP, EST and LAP activities; they were also satisfactory for observing GOT activity. Buffer systems III and IV were not used for detecting these enzymatic activities, except for GOT activity, which gave unfavorable results. Buffer system II was found to be somewhat better than buffer system I for resolving some of the above enzymatic activities. This will be discussed later. Neither buffer systems I and II nor buffer systems III and IV were found capable of detecting enzymatic activities of MDH, ODH, SoDH and XO in the so-called alpha, beta and gamma races of *Tricula aperta* during the course of my study. This might have

TABLE 1. The four buffer systems utilized for detecting various enzymatic activities of the alpha, beta and gamma races of *Tricula aperta* using whole-body pooled samples.

Substrates	Buffer system I	Buffer system II	Buffer system III	Buffer system IV
AAP	+3	+3	ND	ND
AcP	*	*	ND	ND
AlP	+3	+3	ND	ND
EST-1	+3	+3	ND	ND
EST-2	+2	+2	ND	ND
EST-3	+3	+3	ND	ND
GOT	+1	+1	*	*
LAP	+3	+3	ND	ND
MDH	*	*	*	*
ODH	*	*	*	*
SoDH	*	*	*	*
XO	*	*	*	*
αGPDH	*	*	ND	ND
βHBDH	*	*	ND	ND

Abbreviations: EST-1 = α-naphthyl acetate used as substrate; EST-2 = α-naphthyl proprionate used as substrate; EST-3 = β-naphthyl acetate used as substrate; ND = not determined; +1 = satisfactory results; +2 = good results; +3 = excellent results; * = non-satisfactory results (poor resolution or no reaction at all); only one test was performed, except for AcP activity.

been due to inadequate enzymatic activities in the samples used. Buffer systems III and IV were not used for detecting the AcP, LAP, αGPDH and βHBDH activities because of lack of snail samples. Buffer systems I and II were used for detection of these enzymes but were found to be unsatisfactory, except for LAP, for which excellent results were obtained. The resolution of non-specific enzymatic activities of AlP was aided by buffer system II, as shown in Fig. 1. EST non-specific activities resolved by buffer system I using β-naphthyl acetate and by buffer system II using α-naphthyl acetate as the substrates are shown in Figs. 2 and 3, respectively.

The alpha population was designated as a reference for scoring the relative mobilities of electromorphs to the 1.00 band. This method was similar to that used by Hubby & Lewontin (1966), and others. Thus, the slow band of the alpha snails was always assigned the numerical value 1.00 in calculating for relative electromorph mobilities in both single and multi-banded regions of both intra- and interpopulation samples. The independent zones (= presumptive genetic loci) in each enzymatic activity, including relative mobility, were numbered sequentially from the most anodal to the most cathodal zones. The number of zones and the bands of each enzymatic activity, including the relative mobilities of electromorphs detected by buffer systems I and II, are shown in Table 2. The comparative schematic diagrams of various enzymatic bands which showed some differences between the three populations of the alpha, beta and gamma snails are shown in Figs. 4 and 5. Those enzymes were AlP, EST-2, EST-3, EST-4 and GOT, and AlP, EST-1, EST-2, EST-5 and GOT, respectively.

There were 10 zones of presumptive genetic loci (AAP-1, AAP-2, EST-1 to 4, LAP-1, LAP-2 and GOT) and 12 bands (= presumptive alleles) found in the alpha population. However, in both the beta and gamma populations, there were also 10 zones of presumptive genetic loci, but only 11 presumptive alleles (= bands) when buffer system I was used for detecting AAP, AlP, EST, LAP and GOT activities (Table 2). The differences between the alpha, beta and gamma snails could be noticed also from the electromorph mobilities. The slow band in the same region of the same enzymatic activity in the three populations always appeared in the alpha population, while the majority of the medium and fast bands were found in the beta and gamma populations, respectively (Figs. 4, 5). Moreover, the numbers of presumptive alleles in the enzymatic regions also were different between the alpha and beta populations and between the alpha and gamma populations. The alpha population possessed eight single-banded presumptive alleles (AAP-1, AAP-2, EST-1, 2 and 4, GOT, LAP-1 and LAP-2) and two two-banded presumptive alleles (AlP and EST-3); whereas, the beta and the gamma populations possessed nine single-banded presumptive alleles (AAP-1, AAP-2, EST-1 to 4, GOT, LAP-1 and LAP-2) and only one two-banded presumptive allele (AlP) (Table 2).

In comparison with the results obtained from buffer system II, the differences of the

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FIGS. 1-3. Various enzymatic activities of the alpha, beta and gamma races of *Tricula aperta* as detected by buffer systems I and II. FIG. 1. The enzymatic activities of alkaline phosphatase of the alpha, beta and gamma races as detected by buffer system II using β-naphthyl acid phosphate as substrate. Notation above each sample column indicates the snail population sample. The only one recognized zone of presumptive genetic locus is numbered to the right. FIG. 2. The non-specific esterase activities of the alpha, beta and gamma races as detected by buffer system I using β-naphthyl acetate as substrate. The various recognized zones of presumptive genetic loci are numbered to the right. Notation above each sample column indicates the snail population sample. FIG. 3. The non-specific esterase activities of the alpha, beta and gamma races as detected by buffer system II using α-naphthyl acetate as substrate. The various recognized zones of presumptive genetic loci are numbered to the right. Notation above each sample column indicates the snail population sample.

Abbreviations: Af = alpha pooled females only; Am = alpha pooled males only; Ap = alpha pooled males and females; Bf = beta pooled females only; Bm = beta pooled males only; Bp = beta pooled males and females; Gf = gamma pooled females only; Gm = gamma pooled males only; Gp = gamma pooled males and females.

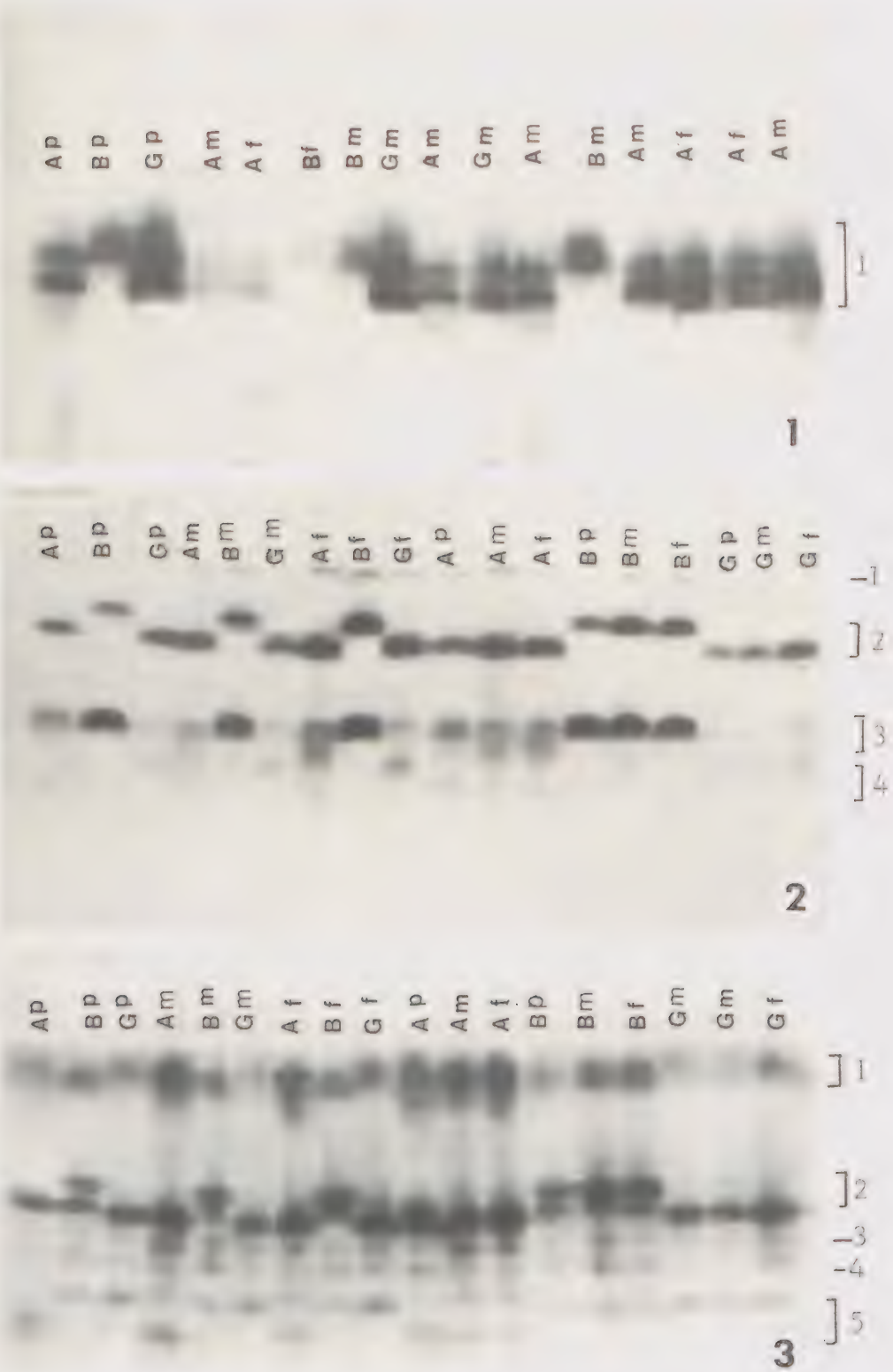
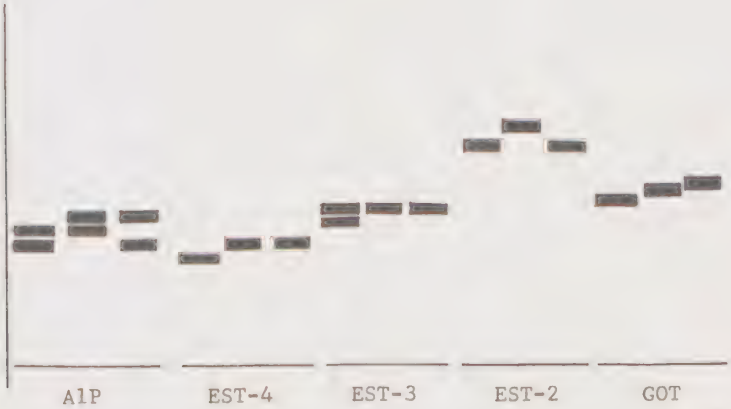
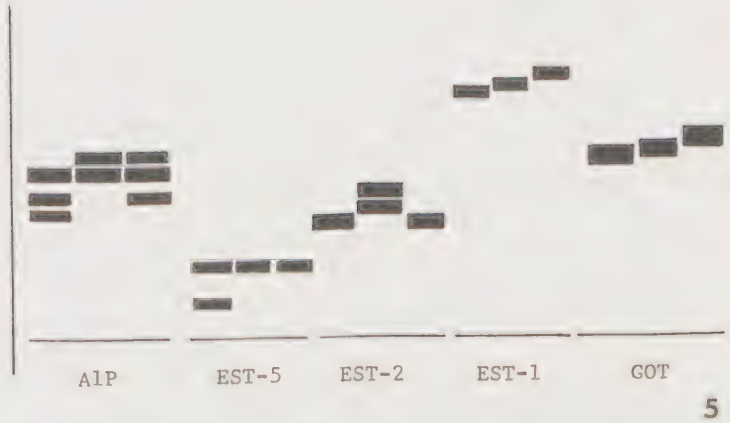

Ap Bp Gp Am Af Bf Bm Gm Am Gm Am Bm Am Af Af Am
1
1
Ap Bp Gp Am Bm Gm Af Bf Gf Ap Am Af Bp Bm Bf Gp Gm Gf
1 2 3 4
2
Ap Bp Gp Am Bm Gm Af Bf Gf Ap Am Af Bp Bm Bf Gm Gm Gf
1 2 3 4 5
3

TABLE 2. Comparison of the mobilities of electromorphs in each presumptive genetic locus of various enzymatic activities in three races of *Tricula aperta* as detected by buffer systems I and II.

Presumptive alleles (= bands)							
Buffer system I				Buffer system II			
Enzymes	Alpha	Beta	Gamma	Enzymes	Alpha	Beta	Gamma
AAP-1	1.00	1.00	1.00	AAP	1.00	1.00	1.00
AAP-2	1.00	1.00	1.00				
AlP	1.00/ 1.14	1.14/ 1.25	1.00/ 1.25	AlP	1.00/ 1.14/ 1.29	1.29/ 1.38	1.14/ 1.29/ 1.38
EST-1	1.00	1.00	1.00	EST-1	1.00	1.05	1.09
EST-2	1.00	1.07	1.00	EST-2	1.00	1.05/ 1.19	1.00
EST-3	1.00/ 1.15	1.15	1.15	EST-3	1.00	1.00	1.00
EST-4	1.00	1.12	1.12	EST-4	1.00	1.00	1.00
				EST-5	1.00/ 2.13	2.13	2.12
GOT	1.00	1.05	1.06	GOT	1.00	1.05	1.07
LAP-1	1.00	1.00	1.00	LAP	1.00	1.00	1.00
LAP-2	1.00	1.00	1.00				
Total	12	11	11	Total	12	11	11

enzymatic activities between the three snail populations were additional strong evidence of significant race differences. The nine presumptive genetic loci (AAP, AlP, EST-1 to 5, GOT and LAP) and 12 presumptive alleles were observed in the alpha population, whereas the beta and the gamma populations both possessed nine presumptive genetic loci (same as in the alpha population), but both beta and gamma races contained 11 presumptive alleles (Table 2). In the multibanded regions, the beta and gamma populations possessed a difference in numbers of presumptive alleles (= bands), e.g., in the AlP activity region the beta population had two bands. Therefore, this is additional evidence supporting the distinctness of the alpha, beta and gamma snails. The differences in numbers of presumptive alleles in some specific enzymatic activity regions between the three populations of the alpha, beta and gamma snails were very pronounced. The alpha population possessed seven single-banded presumptive alleles (AAP, EST-1 to 4, GOT and LAP), one two-banded presumptive allele (EST-5) and one three-banded presumptive allele (AlP). The beta race also had seven one-banded presumptive alleles (AAP, EST-1 and 3 to 5, GOT and LAP) and two two-banded presumptive alleles (AlP and EST-2). On the other hand, the gamma population contained eight single-banded presumptive alleles (AAP, EST-1 to 5, GOT and LAP) and one three-banded presumptive allele (AlP).





FIGS. 4,5. Schematic comparisons of various selected enzymatic patterns in pooled specimens of the so-called alpha, beta and gamma races of *Tricula aperta* as detected by either buffer system I or II. Individual horizontal lines from the left to the right represent the alpha, beta and gamma population samples, respectively. The number of band(s) found in any population is indicated by the number of horizontal line(s) in each column. The enzyme electromorph mobilities are shown in Table 1. FIG. 4. The patterns shown are alkaline phosphatase (AlP), esterase-4 (EST-4), esterase-3 (EST-3), esterase-2 (EST-2) and glutamate oxaloacetate transaminase (GOT), as detected by buffer system I. FIG. 5. The patterns shown are AlP, esterase-5 (EST-5), EST-2, esterase-1 (EST-1) and GOT, as detected by buffer system II.

Presumably, any given presumptive genetic locus of the various enzymatic activities detected by buffer system I for the alpha, beta and gamma snails were comparable (see Figs. 2, 4; Table 2). The alpha, beta and gamma populations shared a single-banded presumptive allele in both AAP-1 and AAP-2 (Table 2); there were not differences in these alleles between the three populations. In AlP activity, there was only one presumptive locus in which three bands were observed: the beta and the gamma populations shared a common first presumptive allele ($1^{1.25}$), whereas the alpha and the beta snails shared a second presumptive allele ($1^{1.14}$), and the third presumptive allele ($1^{1.00}$) was found only in the alpha and gamma populations. Therefore, they were partially different in regard to AlP activity.

The non-specific esterase activities as detected by the β-naphthyl acetate substrate consisted of four presumptive genetic loci which revealed the following characteristics: the esterase

activity of the first region (EST-1) was the same for all three populations; they shared the same common presumptive allele. The second region of esterase activity (EST-2) was composed of two bands; the first band ($2.1^{1.07}$) belonged to the beta population and the second band ($2.2^{1.00}$) was found only in the alpha and gamma populations. The third region, EST-3, was composed of two bands; the first band ($3.1^{1.15}$) was a common presumptive allele of all three populations; the second band ($3.2^{1.00}$) was found only in the alpha population. The fourth region, EST-4, also consisted of two bands: the first band ($4.1^{1.12}$) belonged to the beta and gamma populations; the second band ($4.2^{1.00}$) was found only in the alpha population.

GOT activity was restricted to one presumptive genetic locus with one band for each population. The band of the alpha population was very easily distinguished from those of the beta and gamma populations. But, the bands of the beta and gamma populations were difficult to distinguish clearly from each other since their mobilities were so similar, i.e., 1.05 and 1.06, respectively (Fig. 4 and Table 2).

In comparing the results obtained from buffer systems I and II (Figs. 1, 3-5; Table 2), there were more bands in buffer system II and the bands were more sharply separated. The migration of the electromorphs in the enzymatic activities also were noticeably faster. The alpha, beta and gamma populations shared differences which were not evident from using buffer system I. AAP activity (not shown in Figs. 4 and 5) contained only one presumptive genetic locus, but for some reason its electromorphs moved faster in buffer system II. No differences in AAP activity were seen between the three races of these snails. Buffer system II seemed to give better resolution of AlP activity. An additional slow band was detected from one alpha pooled female sample and an additional fast band was seen from one gamma pooled male/female sample when using buffer system II. The rest of the sample had only two AlP bands. All four bands of this enzymatic activity were assigned to one presumptive genetic locus. The first band ($1.1^{1.38}$) was a common presumptive allele found in the beta and gamma populations. The second band ($1.2^{1.29}$) was found in all three populations. The third band ($1.3^{1.14}$) was common to the alpha and gamma populations. It was not seen in the beta population. The fourth band ($1.4^{1.00}$) occurred only in the alpha population.

Non-specific esterase activities (EST) determined by buffer system II were not much different in result from buffer system I. However, the numbers of bands and their separation were found to be greater when buffer system II was used. Five presumptive genetic loci were observed. Two zones of EST activities (EST-3 and EST-4) were very similar in both number of bands and mobilities in all three snail populations. Each presumptive genetic locus contained a single presumptive allele. The differences in presumptive genotypes (in regard to number of presumptive alleles and mobility of electromorphs) between the alpha, beta and gamma populations were found in EST-1, EST-2 and EST-5. EST-1 contained three bands, one of which belonged to each snail population, i.e., a fast band ($1.1^{1.09}$), a middle band ($1.2^{1.05}$) and a slow band ($1.3^{1.00}$) were observed in the gamma, beta and alpha populations, respectively. There were three presumptive alleles in EST-2. The first two bands ($2.1^{1.19}$ and $2.2^{1.05}$) were found only in the beta population and the third band ($2.3^{1.00}$) was a common band of the alpha and gamma populations. EST-5 comprised two bands; the fast band ($5.1^{2.13}$) was an allele common to all three populations and the slow band ($5.2^{1.00}$) was seen only in the alpha population.

There was an interesting phenomenon in regard to the GOT activity found in the three populations. A three-banded region was observed, yet none of the three populations shared any presumptive alleles at this locus. The fast band ($1.1^{1.07}$) or the first presumptive allele belonged to the gamma population. The second or middle band ($1.2^{1.05}$) was a component of the beta population, and the third or slow band ($1.3^{1.00}$) was seen only in the alpha population. This phenomenon might be related to the susceptibilities of the snails to the infection of the Mekong schistosome, and may be additional supportive evidence indicating specific distinctness of each of the populations.

The final enzymatic activity that could be detected by buffer system II during my study was LAP. There was only one presumptive genetic locus, and no differences in LAP activity were seen between the alpha, beta and gamma populations.

Further details of individual enzymatic activities follow.

Alanine aminopeptidase (AAP), buffer systems I and II. Two regions of alanine aminopeptidase activity were detected by buffer system I. Each region contained only a single band. AAP-1 was a broader band in comparison with AAP-2. These two bands were close to each other in position on the gel. AAP-2 stained very slightly. For buffer system II, only a single band of AAP activity was detected. There were no differences between the three races of *Tricula aperta* as far as this enzymatic activity was concerned.

Acid phosphatase (AcP), buffer systems I and II. Neither buffer system gave favorable results with this enzyme. A zone approximately 2 cm wide comprising few bands of non-specific acid phosphatase activities could be recognized but, because of overlapping, distinct bands were difficult to recognize. Also, the stain was too light. These problems may have been due to an unsuitable buffer system, technical staining problems or excessive alkaline phosphatase activity in the samples.

Alkaline phosphatase (AlP), buffer systems I and II. A zone of non-specific alkaline phosphatase activity was detected by each buffer system. The number of bands and electromorph mobilities were somewhat different from population to population (inter- and intrapopulation) and according to the buffer system. One region of non-specific alkaline phosphatase activity comprising three bands could be recognized with buffer system I. Each population contained only two bands. There was no single band that was common to all three populations when this buffer system was used. However, two bands of each population were shared individually by the other two populations, i.e., the fast band (1.25) was common to the beta and gamma populations, the middle band (1.14) was shared by the alpha and beta populations and the slow band (1.00) occurred in both alpha and gamma populations.

Only one zone of non-specific alkaline phosphatase activity was detected by buffer system II. In this way it was similar to buffer system I. However, of the two systems, buffer system II seemed to be more efficient for resolving AlP activity, because by using it an additional band could be seen in two of the populations, i.e., one more band could be detected from an alpha female sample (which was considered to be a slow band), and one more band was detected from a pooled male/female gamma sample (this band was considered to be a fast band). Therefore, four AlP bands were recognized in buffer system II. Three bands, two bands and three bands were found in the alpha, beta and gamma populations, respectively. A common band for the three races was found at the medium-fast band (1.19). The slow-medium band (1.14) was common to the alpha and gamma populatons, and the fast band (1.38) was common to the beta and gamma populations. The slow band (1.00) was seen only in the alpha population.

Esterase (EST), buffer systems I and II. The results of non-specific esterase activities detected by buffer systems I and II were quite distinctive. These two buffer systems seemed to be equally good for resolving EST activity in the three races of *Tricula aperta*. Both buffer systems permitted sharp band segregations and staining. However, the number of bands and enzymatic activity regions were somewhat different. Four zones of non-specific esterase activities were detected by buffer system I. The number of bands in the alpha, beta and gamma populations were five, four and four, respectively. EST-1 was composed of a single band; there were no differences between the three populations. EST-2 contained two bands: the fast band ($2.1^{1.07}$) belonged to the beta population, and the slow band ($2.2^{1.00}$) was found in both the alpha and gamma populations. EST-3 comprised two bands: the fast band ($3.1^{1.15}$) was common to the three populations; the slow band ($3.2^{1.00}$) was seen only in the alpha population. EST-4 also contained two bands: the fast band ($4.1^{1.12}$) was a common presumptive allele between the beta and the gamma populations, while the slow band ($4.2^{1.00}$) was found in the alpha population alone. No intrapopulation differences were

found between pooled female samples and pooled male samples.

The esterase bands separated somewhat better in buffer system II than in buffer system I, even though some streaks were seen between the bands in the zones of non-specific EST activity. These latter streaks did not seem to hinder band identifications. Five regions of non-specific EST activity were observed. Six bands occurred in the alpha and beta populations, whereas only five bands were seen in the gamma population. The first region of EST activity (EST-1) comprised three bands. No common band was observed between any two populations; the electromorph mobilities were all different in the three populations. The fast band ($1.1^{1.09}$), the medium band (= middle band) ($1.2^{1.05}$) and the slow band ($1.3^{1.00}$) were components of the gamma, beta and alpha populations, respectively. EST-2 was composed of three bands, i.e., the fast band ($2.1^{1.19}$) and the medium band ($2.2^{1.05}$) belonged to the beta population only. The slow band ($2.3^{1.00}$) was common to both the alpha and gamma populations. EST-3 contained only one band (not shown in Fig. 5); there was no difference between the three populations – they all shared the same common presumptive allele. EST-4 was the same as EST-3. The last zone, EST-5, comprised two bands. The fast band ($5.1^{2.13}$) was a common presumptive allele of all three populations, whereas the slow band ($5.2^{1.00}$) was recognized in the alpha population. No intrapopulation differences were found in the pooled female samples or pooled male samples.

Glutamate oxaloacetate transaminase (GOT), buffer systems I, II, III and IV. A single-banded region of GOT activity was detected in each population of the alpha, beta and gamma snails by buffer systems I and II. However, their electromorph mobilities were somewhat different. For buffer system I, the mobility rates of the electromorphs of the alpha, beta and gamma populations were 1.00, 1.05 and 1.06, respectively. Actually, the mobility of the electromorphs of the beta and gamma populations were almost identical. In buffer system II, the mobility of the electromorph of the gamma population tended to migrate relatively faster than those of the alpha and beta populations. The mobility rates of the alpha, beta and gamma populations in buffer system II were 1.00, 1.05 and 1.07, respectively. No intrapopulation variation in GOT activity was found.

The results obtained for GOT from buffer systems III and IV are inappropriate to describe because the reactions were too light, and only a single run was performed for each system. Inadequate results were also obtained when sliced gels from these runs were stained for MDH, ODH, SoDH and XO activities. The poor results may have been due to inadequate amounts of these enzymes present in the prepared samples. Therefore, further efforts to detect these enzymatic activities should be made at a later date when more samples are available.

Leucine aminopeptidase (LAP), buffer systems I and II. Two and one zones of LAP activity were detected by buffer systems I and II, respectively. All results were the same as for AAP activity described previously. The location of LAP activity was also the same as that for AAP activity. However, the stains appeared to be somewhat darker in both buffer systems for LAP activity than for AAP activity. No intrapopulation variation was found in relation to this enzymatic activity.

Malate dehydrogenase (MDH), buffer systems I, II, III and IV. No satisfactory results were obtained from any of the buffer systems. A very light blurred zone of MDH activity was seen in all four buffer systems. Therefore, more tests should be made in the future for this enzyme.

Octanol dehydrogenase (ODH), buffer systems I, II, III and IV. None of the buffer systems showed any reactions for ODH. No artifacts, i.e., over-staining or streaks, occurred to hinder observation.

Sorbital dehydrogenase (SoDH), buffer systems I, II, III and IV. The results were the same as for ODH activity, i.e., no enzymatic reactions were detected.

Xanthine oxidase (XO), buffer systems I, II, III and IV. XO activity was not very clear in

any of the buffer systems. A light single zone of XO activity was seen in buffer system I. However, the reaction was not strong enough to be able to compare the alpha, beta and gamma populations.

α-glycerophosphate dehydrogenase (αGPDH), buffer systems I and II. Due to poor resolution, no satisfactory results were obtained for αGPDH. The precipitation of stain rendered the samples uninterpretable.

β-hydroxybutyrate dehydrogenase (βHBDH), buffer systems I and II. The resolution for βHBDH activity was very poor. One zone of βHBDH activity, however, was noticeable in both buffer systems, but the reaction was not clear. It was hindered by some streaks and by over-staining. Therefore, the βHBDH activity from each snail population could not be compared.

DISCUSSION

A total of 12 enzymes, viz., AAP, AcP, AlP, EST (using three different substrates), GOT, LAP, MDH, ODH, SoDH, XO, αGPDH and βHBDH, were selected for studying enzymatic activities in the alpha, beta and gamma races of *Tricula aperta*. Four different buffer systems were used in the studies. Buffer systems I and II were excellent for resolving the enzymatic activities of AAP, AlP, EST (with substrates 1 and 3; see Table 1) and LAP; they gave good results for detecting EST (with substrate 2), and they were satisfactory in resolving GOT activity. Buffer systems III and IV were not used to detect these enzymatic activities, except for GOT activity, and here the results were not satisfactory. Neither buffer systems I and II nor buffer systems III and IV were capable of detecting the enzymatic activities of MDH, ODH, SoDH and XO in these snails. However, only a single experiment was performed for studying their activities in each buffer system. Buffer systems III and IV were not used for detecting AcP, LAP, αGPDH and βHBDH. However, the activities of these enzymes, except for LAP, were not adequately resolved in buffer systems I and II.

The results of these electrophoretic studies showed some evidence of genotypic differences between the three races of *Tricula aperta*. Enzymatic activities of AlP, EST and GOT revealed similarities and differences in numbers of presumptive alleles and in the mobility rates of the electromorphs to be compared at the same presumptive genetic locus.

For AlP activity, as detected by buffer system I, only a single presumptive genetic locus was observed for all three races of snails. The locus contained two presumptive alleles. There were no differences in numbers of alleles found between the three races of *Tricula aperta*. But, obvious differences easily could be distinguished in the rates of electromorph mobilities. The alpha race, which was used as reference for calculating the mobility rates throughout my study, contained a slow (1.00) and a medium (middle) (1.14) band, whereas the beta race had a medium band (1.14) and a fast band (1.25), and the gamma race had a slow band (1.00) and a fast band (1.25). Therefore, there was no common allele between all three races of these snails. A common allele was shared between any two of the three races: alpha and gamma shared the slow allele, alpha and beta shared the medium allele, and beta and gamma both had the fast allele. Thus, as far as AlP activity is concerned, recognition of the alpha, beta and gamma snails as only races of *T. aperta* as proposed by Davis et al. (1976) may not be correct. They may be sibling species rather than races. Other information presented later in the text also has a bearing on this problem.

When buffer system II was used for detecting AlP activity, an additional band was detected from both alpha and gamma populations. Presumably, this extra band came from the females (see Figs. 1, 5). Therefore, the assigned presumptive genetic locus for this enzymatic activity was composed of four presumptive alleles (= bands): the first or fast band ($1.1^{1.38}$) was a common presumptive allele of the beta and gamma snails; the second or medium-fast band ($1.2^{1.29}$) was a common presumptive allele of all three populations of snails; the third

or slow-medium band ($1.3^{1.14}$) was a common presumptive allele of the alpha and gamma snails; and the fourth or the slow band ($1.4^{1.00}$) belonged to the alpha population only. Thus, the results of my study using buffer system II for resolving AlP activity provided further evidence indicating that these snails are genetically dissimilar. The beta snails are especially different, lacking two alleles. Although the numbers of alleles were equal in the alpha and gamma snails, they were still genotypically different, because the alleles found in these two races were at distinctly different locations. The variant of the alpha snails appeared in the slow band, whereas it was found in the fast band in the gamma snails.

There were four zones of presumptive genetic loci when buffer system I was applied for detecting non-specific EST activities. The first presumptive genetic locus appeared to be identical in all three snail populations. It comprised a single presumptive allele. The major differences were seen in EST-2, 3 and 4. EST-2 was composed of two bands. The fast band ($2.1^{1.07}$) was seen in the beta only, whereas the slow band ($2.2^{1.00}$) was common to the alpha and gamma snails. Therefore, the beta snails were obviously different genetically from the alpha and the gamma snails as far as EST-2 was concerned. For EST-3, which contained two bands, the phenotype was somewhat different from that shown by EST-2. The fast band ($3.1^{1.15}$) was a common band of the three populations, while the slow band ($3.2^{1.00}$) was observed only in the alpha snails. Therefore, this indicated that the alpha snails were genotypically dissimilar to the beta and gamma snails. Moreover, the differences between the alpha and the gamma snails could be noticed in EST-4. EST-4 also contained two bands. Again, the slow band was seen only in the alpha population. Its fast band ($4.1^{1.12}$) was not present in the alpha snails, but it was common to both the beta and the gamma snails. No intrapopulation variation of EST activity was seen. Undoubtedly, the results of my study for non-specific esterase activities using buffer system I gave strong evidences of genotypic differences between the alpha, beta and gamma snails. This may mean that the three are different species.

The same type of study of non-specific esterases, but using buffer system II, gave similar results. However, this buffer system resolved more bands and it was easier to recognize the differences between the alpha, beta and gamma snails. Obviously, buffer system II was somewhat better for resolving the non-specific esterase activities in these hydrobiid snails than was buffer system I. (This is completely contrary to the results obtained for the pulmonate *Biomphalaria* spp. from the Middle East (Rudolph, pers. comm.).)

Thus, using buffer system II, five zones of presumptive genetic loci were determined for the three *Tricula* populations. The differences which could be recognized in these non-specific EST activities occurred in EST-1, 2 and 5 (Fig. 5). The other genetic loci, i.e., EST-3 and 4, were identical. EST-1 contained three bands, a fast band ($1.1^{1.09}$), a medium band ($1.2^{1.05}$) and a slow band ($1.3^{1.00}$), which belonged to the gamma, beta and alpha snails, respectively. In this respect, the three populations were all different. EST-2 also contained three bands. The first two bands, the fast band ($2.1^{1.09}$) and the medium band ($2.2^{1.05}$) were seen only in the beta snails, but the third band or slow band ($2.3^{1.00}$) was common to the alpha and gamma snails. Therefore, in regard to this presumptive genetic locus, the beta snails were genotypically different from the other two races of *T. aperta*. EST-5 comprised only two bands. The fast band ($5.1^{2.13}$) was common to all three races. The slow band ($5.2^{1.00}$) appeared only in the alpha snails. No intrapopulation variation was found in the numbers of alleles. On the basis of this presumptive genetic locus, the alpha snails are genetically different from the beta and the gamma snails.

Wurzinger (pers. comm.) suggested that GOT activity might be involved in the susceptibility of African bulinine snails to infection with *Schistosoma haematobium* (Bilharz), since he found a possible positive correlation between the GOT enzyme electromorph mobilities and susceptibilities to various strains of *S. haematobium*. He found that all susceptible polyploids possessed the slow electromorph, whereas diploid snails known to be refractory possessed the fast electromorph. However, not all diploid species of *Bulinus* are insusceptible to

this schistosome infection (Lo et al., 1970), and the manner in which the different GOT electromorphs may be related to the susceptibility of the snails to the parasite is not known. Since schistosome cercariae are extracellular parasites, they develop in the hepatopancreatic haemocoel. Presumably, they obtain all of their nutrients from the host hemolymph, including amino acids essential for growth. If these and all other factors are met, development of the cercariae in the snails will proceed normally. If one important factor is insufficient, e.g., the amount of essential free amino acids in the snail hemolymph (presumably controlled by GOT), cercariae will have difficulty in growing. The GOT electromorph differences may be involved in such a deficiency since GOT is related to carbohydrate and amino acid metabolism.

The results of my study showed that the degree of susceptibility to *Schistosoma mekongi* Voge, Bruckner & Bruce also may be correlated to GOT mobility, although the mobility/susceptibility correlation is reversed from Wurzinger's. That is, I found that the *Tricula* snails which possessed the fast electromorph (gamma race) were more susceptible to *S. mekongi* than were the ones that possessed the slow electromorph (alpha race). However, the beta snails which had demonstrated the highest susceptibility to *S. mekongi* (Sommani, 1976; Liang & Kitikoon, 1980; Kitikoon, 1981b) possessed the medium electromorph. But, since all races are susceptible to some degree to *S. mekongi*, the possible influence of GOT on susceptibility is less obvious, but still possible.

In analyzing GOT activity using buffer systems I and II, similar results were obtained. There was one zone (presumptive genetic locus) comprising three bands. The gamma snails possessed the fast band ($1.1^{1.06}$), the beta snails the medium band ($1.2^{1.05}$) and the alpha snails the slow band ($1.3^{1.00}$), as detected by buffer system I. The same was found with buffer system II, where the fast band ($1.1^{1.07}$), the medium band ($1.2^{1.05}$) and the slow band ($1.3^{1.00}$) belonged to the gamma, beta and alpha snails, respectively. Again, the results observed in regard to GOT activity indicated genotypic differences between these three races of *Tricula aperta*. Further studies on GOT activity and susceptibility should be undertaken to give a more definite answer regarding possible correlation and cause/effect between the two.

LAP activity gave two bands with buffer system I, but only one band with buffer system II. The results from using buffer system II were not really satisfactory. Except for this activity, buffer system II gave better results than did buffer system I throughout the study. Additional studies should be made to improve the results with LAP activity from buffer system I. No differences between the alpha, beta and gamma snails were seen with either buffer system. However, further studies with these enzymes might prove fruitful.

Similar to these studies, but using polyacrylamide disc gel electrophoresis to compare foot muscle esterases of diploid and tetraploid *Bulinus*, Burch & Lindsay (1967) found that the diploid individuals were characterized by two deep staining fast bands and the tetraploid individuals by a single fast band. Wright (1971) indicated that both esterase and acid phosphatase isoenzymes were found to be useful for distinguishing the two diploid species from Madagascar. Wu (1972) showed that the electrophoretically separated foor muscle esterases of F_1 hybrids are a combination of the two parental patterns. Therefore, the electrophoretic results obtained from my present study provide evidence to support the contention that the so-called alpha, beta and gamma "races" of *Tricula aperta* are at least distinct subspecies and may well be different species.

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EFFECTS OF VARIOUS TYPES OF FOOD AND MUD PREPARATIONS ON SURVIVORSHIP AND EGG PRODUCTION OF *BITHYNIA SIAMENSIS SIAMENSIS* (PROSOBRANCHIA: BITHYNIIDAE)[1]

M. Kruatrachue, S. Ratanatham, S. Jantataeme and E.S. Upatham

ABSTRACT

Effects of various types of food such as synthetic snail food and diatoms on survivorship and egg production of *Bithynia siamensis siamensis* was studied. Survivorship was found to be best in snails fed with both synthetic snail food and diatoms. Greatest egg production was found in the snails fed with both synthetic snail food and diatoms.

Effects of different types of mud preparations (mud alone, mud with 6% $CaCO_3$, and mud with 12% $CaCO_3$) on survivorship and fecundity of the snails also were studied. Survivorship was not affected by the types of mud used, although egg laying was affected. The largest number of eggs was laid in culture with mud alone, less with mud with 6% $CaCO_3$ and smallest with mud with 12% $CaCO_3$.

INTRODUCTION

Opisthorchiasis, a liver disease of man caused by the liver-fluke *Opisthorchis viverrini* (Poirier), is endemic in the northeastern part of Thailand. Published information on the parasite concerns the life cycle (Wykoff et al., 1965), taxonomy of intermediate hosts (Brandt, 1974), parasite surveys (Sadun et al., 1955; Harinasuta & Vajrasthira, 1960), pathological features (Tansurat, 1971; Viranuvatti & Stitnimankarn, 1977; Chainuvati et al., 1976; Bhamarapravati et al., 1978) and clinical drug trials (Harinasuta et al., 1966; Wykoff et al., 1967; Bunnag et al., 1970; Muangmanee et al., 1974). Still, there is a lack of information in several areas, such as snail bionomics and population dynamics, snail ecology, snail-parasite relationships, etc., which are critical for practical purposes in the disease control.

One of the major obstacles impeding research in opisthorchiasis has been the unavailability of laboratory-bred snails that are the first intermediate host of *Opisthorchis viverrini*. It often is difficult to maintain the snails in the laboratory owing to the lack of appropriate food and substrate. Thus, we report on effects of various types of food and mud preparations on survivorship and egg production in an operculate snail, *Bithynia siamensis siamensis* Lea, the first intermediate host of *O. viverrini* in the central part of Thailand.

MATERIALS AND METHODS

All *Bithynia siamensis siamensis* used in these studies were collected from the field (Bangna, Bangkok, Thailand). Voucher specimens have been deposited in the Museum of Malacology, Mahidol University.

Effects of various types of food on survivorship and egg production of *Bithynia siamensis siamensis*

The following types of food were used to feed the snails: synthetic snail food (powdered rice (21 g), powdered dried leaves of *Leucaena glaura* (Leguminosae) (21 g), powdered milk (7 g), multivitamin complex (3 g), $CaCO_3$ powder (1 g), agar (0.1 g) and distilled water (400 ml); see Sumethanurugkul, 1970); diatoms, *Achnanthes exigua* (see Bruce et al., 1971); and synthetic snail food and diatoms.

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Twenty small, round plastic containers, measuring 11 cm in diameter and 6 cm in height, were used to contain snails for each type of food experiment. For the snail substrate, a thin layer of powdered mud baked at 160°C for 6 hr was put into the container; thereafter, 300 ml of conditioned water was added. Four males and six females were placed in each container.

For the synthetic snail food experiment, each container received approximately 1-2 ml of synthetic snail food daily. For the diatom experiment, 5 ml of 5% suspension of diatoms was added to each container twice a week. For the synthetic snail food and diatom experiment, each container received 1-2 ml of synthetic snail food daily and 5 ml of 5% suspension of diatoms once a week.

Effects of various types of mud preparations on survivorship and egg production of *Bithynia siamensis siamensis*

To test the effects of various mud types used for culturing snails, the following types of mud were used: mud; mud with 6% $CaCO_3$ (by weight); and mud with 12% $CaCO_3$ (by weight).

The mud was crumbled into small pieces, placed in an oven and baked for 5 hr at 160°C to dry. Next, the dried mud was ground into coarse powder, and the $CaCO_3$ powder was added to and mixed with the powdered mud. Then, the mud was put in the oven at 160°C for another 4 hr to kill most unwanted organisms.

Four males and six females in each container were cultivated in each of 60 small, round plastic containers (11 cm in diameter and 6 cm in height). Twenty containers were used for each type of mud experiment. Each container received 1-2 ml of synthetic snail food (Sumethanurugkul, 1970) daily and 5 ml of 5% suspension of diatoms (Bruce et al., 1971) once a week.

Survivorship of the snails was observed weekly. In addition, the time of egg-laying and the number of eggs and young snails produced were recorded for each container.

RESULTS AND DISCUSSION

Effects of various types of food on survivorship and egg production of *Bithynia siamensis siamensis*

The results clearly indicated that the appropriate type of food was a very important factor in determining both the survivorship and fecundity of the snails. As shown in Table 1, survivorship was best among the snails fed with synthetic snail food and diatoms (85% survival), slightly less among the snails fed with synthetic snail food alone (80% survival), an least among the snails fed with diatoms alone (5% survival). Most of the snails fed with only diatoms died during the first month of the experiment.

When fecundity was expressed in terms of number of eggs laid, it was apparent that those snails fed with synthetic snail food and diatoms produced more eggs than those fed with synthetic snail food alone. There were no eggs produced from snails fed with only diatoms,

TABLE 1. Effects of food on survivorship and production of eggs and young of *Bithynia siamensis siamensis* during a four-month period.

Survivorship and production of young	Types of food		
	Synthetic snail food	Diatoms	Synthetic snail food & diatoms
Adult snail survival rates (%)	80	5	85
Total number of containers with eggs out of 20 containers	6	0	13
Total number of eggs produced	82	0	141
Total number of young snails collected	65	0	120

since most of the snails died in early stages. For the survival of young snails, it was observed that the most critical period was during the first two weeks after hatching. It was during this period that most mortality occurred.

Effects of various types of mud preparations on survivorship and egg production of *Bithynia siamensis siamensis*

For each type of mud preparation, 20 containers with 10 snails each were used. The data were collected for a period of four months (Table 2). Survivorship was generally good in all three types of mud preparations used, with approximately 80-85% of snails surviving at the end of the four-month period. Most of the snails that died presumably did so because of the overgrowth of ostracods, the small crustaceans which are very harmful to snails.

TABLE 2. Effects of mud preparations on survivorship and production of eggs and young of *Bithynia siamensis siamensis* during a four-month period.

Survivorship and production of young	Type of preparation		
	Mud alone	Mud & 6% $CaCO_3$	Mud & 12% $CaCO_3$
Adult snail survival rates (%)	82	84	80
Total number of containers with eggs out of 20 containers	8	6	5
Total number of eggs produced	102	84	68
Total number of young snails collected	80	65	52

In terms of the production of eggs during the four-month period, there was a noticeable difference among various mud preparations. Containers with mud alone were most suitable for egg production; containers with mud and 6% $CaCO_3$ were less so, and those with mud and 12% $CaCO_3$ were least suitable. Altogether, 102 eggs were laid in containers with mud alone, 84 eggs in containers with mud and 6% $CaCO_3$, and 68 eggs in containers with mud and 12% $CaCO_3$.

The total numbers of young collected at the end of the four-month period were different, viz., 80 in containers with mud alone, 65 in containers with mud and 6% $CaCO_3$, and 52 in containers with mud and 12% $CaCO_3$. Most deaths of young snails occurred within two weeks after hatching. A few snails died during the later stages, apparently because of the overgrowth of ostracods.

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A CULTURE METHOD FOR *BITHYNIA* (PROSOBRANCHIA: BITHYNIIDAE), SNAIL HOSTS FOR THE TREMATODE *OPISTHORCHIS VIVERRINI*[1]

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S. Vichasri and E.S. Upatham

ABSTRACT

Two species and a subspecies of *Bithynia* (*B. siamensis siamensis, B. s. goniomphalos* and *B. funiculata*) were cultured in the laboratory with the use of a plastic container provided with mud. The snails were fed with high protein synthetic snail food as the major food source. This food was supplemented with diatoms once a week. The development period for the snail eggs was about 10-12 days, the young grew to maturity in 16-17 weeks, and egg laying followed two to three weeks later. The whole cycle took approximately four to five months. The eggs were laid three to eight in number in a small single row or in double rows. The newly hatched young snails were 0.5-0.8 mm in shell length, and the full-grown snails were 6.5-7.0 mm long for *B. siamensis siamensis* and *B. s. goniomphalos* and 10.5 mm long for *B. funiculata.*

INTRODUCTION

Bithynia siamensis Lea, a freshwater snail, is the natural first intermediate host of the human liver fluke *Opisthorchis viverrini* (Poirier), a parasite (Trematoda: Opisthorchiidae) which afflicts a great number of people in the northeastern part of Thailand. *B. funiculata* Walker, a related species from certain northern provinces, has been infected experimentally with miracidia of *O. viverrini* (Brandt, 1974).

Bithynia siamensis is represented in Thailand by two subspecies, *B. s. siamensis* and *B. s. goniomphalos* (Morelet). The main differences between these two are their distributions and shell morphologies. *B. s. siamensis* and *B. s. goniomphalos* are found in the central and northeastern parts of Thailand, respectively. The distribution of *B. s. siamensis* includes suburban areas of Bangkok, where it is found in ponds and roadside ditches. *B. s. siamensis* is smaller (average adult shell length = 10 mm) and its shells are only slightly eroded when old, while the larger *B. s. goniomphalos* (average adult shell length = 12 mm) has very eroded and dull shells when old (Brandt, 1974).

Bithynia funiculata, the largest of the three taxa, is found in the northern part of Thailand. Its shell differs from the other species in its length (10-15 mm) and in its open, funnel-shaped umbilicus which is surrounded by a thread-like keel (Brandt, 1974).

Because of the role of snails in the transmission of opisthorchiasis, it is important to gain information on the life cycle of *Bithynia*. Cultivation of these snails in the laboratory has not been successful previously, and that deficiency has been one of the main factors impeding research activities on snail-parasite relationships. The purpose of this paper is to report studies on laboratory cultivation of *B. siamensis siamensis, B. s. goniomphalos* and *B. funiculata*, which includes the methods, growth rates of young snails, and mass production of laboratory-bred snails.

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[1]This investigation was supported by the United Nations Development Programme/World Bank/World Health Organization Special Programme for Research and Training in Tropical Diseases. Address reprint requests to E.S. Upatham.

MATERIALS AND METHODS

In general, all three *Bithynia* were cultured with the same techniques. *B. siamensis siamensis* was collected from ponds in Suanphu, Bangkok, *B. s. goniomphalos* from Kalasin, northeastern Thailand, and *B. funiculata* from Lampang, northern Thailand. Voucher specimens have been deposited in the Museum of Malacology, Mahidol University.

Aquaria for maintenance of *Bithynia*

The aquaria for maintenance of *Bithynia* were equipped with aeration pumps, plastic tubes and air stones. Forty-watt cool fluorescent lamps were fixed to the shelves of the units approximately 25 cm above the containers in order to stimulate the growth of diatoms. Snail cultures were maintained with 8 hr of fluorescent light per day.

Environmental conditions

Aged tap water of pH 7.0-7.2 (standing for at least two days) was used for rearing snails. The water temperature was maintained at 27-28°C (air-conditioned room temperature). Water levels in snail containers, aeration, water and room temperatures were checked daily.

Culturing parent snails

A proper mud substrate is important for culturing *Bithynia* species (Kruatrachue et al., 1982). In preparation for mud cultures, only the top 4-5 cm of rich brown top soil was shoveled from the river banks above the water level. All foreign objects were removed from the mud collected. The mud was then crumbled into small pieces, put in the pan, and placed in an oven and baked for 5 hr at 160°C to dry. The dried mud was then crumbled, ground into coarse powder and put in the oven at 160°C for an additional 4 hr in order to kill any remaining living organisms.

To prepare the culture substrate, the baked mud powder was put into a plastic container (22 cm in diameter and 9 cm in height) just to fill its bottom (about 1 cm thick). The container was then filled with conditioned tap water up to 2/3 of its height, and left overnight to let the mud settle to the bottom.

Twelve adult males and 18 adult females were introduced into each breeding culture. Altogether, 12 breeding cultures with a total of 360 snails were used for each of the taxa. The male snails can be distinguished from the females by the presence of a verge or penis on the right side of the neck. The method of Wang & Fan (1972) for *Oncomelania* was used to determine sex for *Bithynia*. The males were marked with fingernail polish to indicate their gender. In the event of death while in culture, the sex of the dead snail was easily determined.

Two types of food were given to the snails: high-protein synthetic snail food[2] (Sumethanurugkul, 1970) and diatoms (Bruce et al., 1971). Cultures of adult snails received approximately 1-2 ml of synthetic snail food daily as a major food source. Diatoms (5 ml of 5% suspension) were given once a week as a supplement.

Culturing young snails

Approximately two to three weeks after the introduction of adult snails to the breeding cultures, the first eggs were laid in small single or double rows of three to eight eggs on the mud surface or on the sides of the containers. After the eggs hatched, as many offspring as possible were removed to prevent the container from becoming overcrowded.

The preparation of cultures for rearing young snails was nearly the same as that described for the culturing of parent snails; small plastic containers (11 cm in diameter and 6 cm in height) were used, each with a density of 20-25 snails. The young snails were fed with synthetic snail food daily and with diatoms weekly as described in the foregoing section.

Measurement of growth

The shell lengths of the young snails were measured once a week under a dissecting microscope. These measurements provided data necessary for comparing the growth rates of the three *Bithynia*.

Termination of breeding cultures of *Bithynia*

The fecundity of breeding snails decreased with time. The cultures were terminated under the following adverse circumstances: persistent overgrowth of green algae and fungi; unexpected high mortality due to deteriorated and accumulated waste; low production of young; appearance of harmful organisms, such as ostracods and various large protozoa.

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[2]Synthetic snail food: powdered rice (21 g), powdered dried leaves of *Leucaena glaura* (Leguminosae) (21 g), powdered milk (7 g), multivitamin complex (3 g), $CaCO_3$ powder (1 g), agar (0.1 g) and distilled water (400 ml).

RESULTS AND DISCUSSION

Culture types

The culture methods for the aquatic snail *Bithynia* are distinctly different from those for *Oncomelania* snails, which are amphibious in nature. Van der Schalie & Davis (1968) found that, among the various vivaria tested, the medium clay pot with little water and aeration provided the best environment for maintaining adult *Oncomelania* and encouraging the production of young. French (1974, 1977), however, reported that plastic containers of 9-15 cm in diameter and 4-5 cm in height were the best for maintaining adult snails and the production of young.

For *Oncomelania* culturing, the mud mound in the center of the dish or the mud ring along the periphery of the dish are essential due to the amphibious nature of the snails (van der Schalie & Davis, 1968; French, 1974, 1977). For *Bithynia*, the most suitable substrate is a thin layer of mud powder which is just enough to cover the bottom of the plastic container.

Eggs and newly hatched snails

Adult snails of all three *Bithynia* were observed to lay eggs on the inner sides of the plastic containers or on the mud. The transparent eggs had an average diameter of 0.5 mm, and were either grouped in a row of three to eight or sometimes were grouped in double rows of six to seven. Within the egg, a one-celled embryo of whitish color was suspended. It underwent cell division until it could be recognized as a shelled infant snail. At this stage, the embryo was colorless, approximately half the size of the egg. In six to seven days, the embryo grew larger, approaching the size of the egg. The eggs hatched and the young snails emerged in 10-12 days.

The patterns of egg laying differ between *Bithynia* and *Oncomelania*. The eggs of *Bithynia* are laid in one to two rows of three to eight and are found on the inner sides of containers, whereas those of *Oncomelania* are laid singly, covered with a soil jacket and deposited

FIG. 1. Progressive appearance in growth of shell length in the three taxa of *Bithynia*: *B. siamensis siamensis* (Fig. 1A), *B. s. goniomphalos* (Fig. 1B) and *B. funiculata* (Fig. 1C). The three stages of growth in shell length are presented from left to right: adult snails, 10-week old snails and 3-week old snails, respectively. Measurement line in mm.

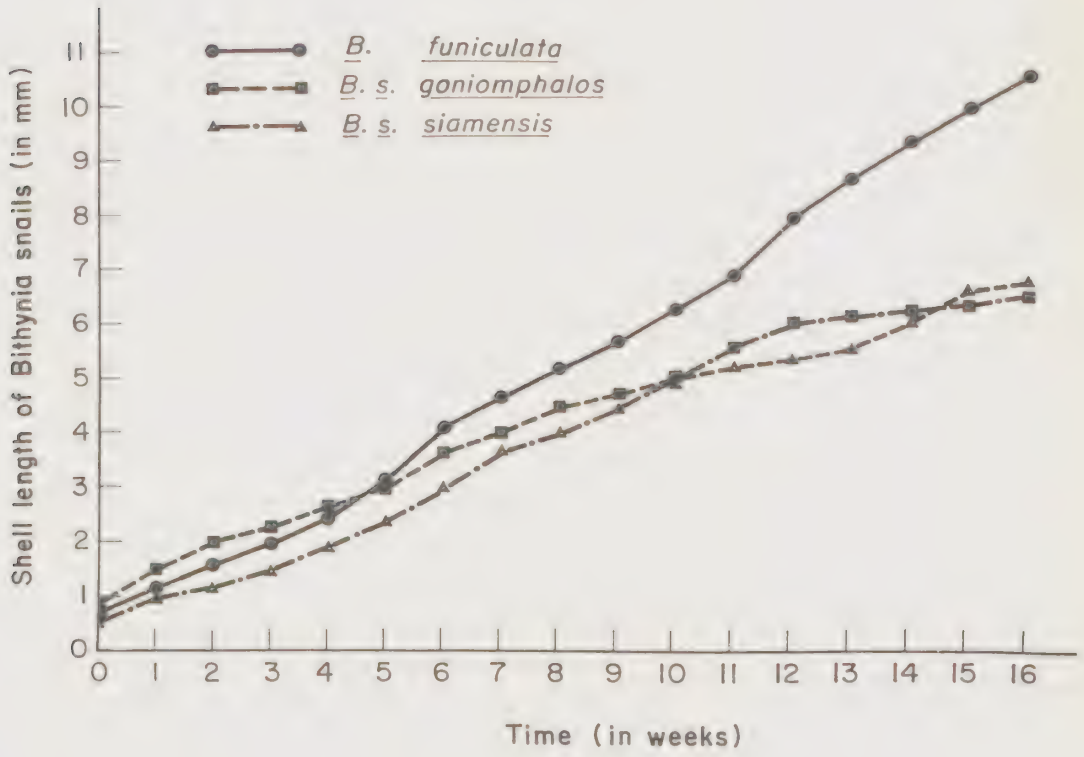

FIG. 2. Growth curves for the three taxa of *Bithynia*: *B. siamensis siamensis, B. s. goniomphalos* and *B. funiculata.*

on soil or other objects such as sticks or rocks (van der Schalie & Davis, 1968). The hatching time for *Bithynia* is much shorter than that for *Oncomelania*. The eggs of *Bithynia* hatched within 10-12 days, but those of *Oncomelania* might take 20-30 days after being laid.

Growth of *Bithynia*

Figure 1 shows the progressive appearance in growth of shell length in the three taxa: *Bithynia siamensis siamensis* (Fig. 1A), *B. s. goniomphalos* (Fig. 1B) and *B. funiculata* (Fig. 1C), respectively. Figure 2 shows the progressive growth of F_1 shell length of the three taxa of *Bithynia*. The newly hatched young snails of the three species were 0.5-0.8 mm in shell

length, and the full-grown snails were 6.5-7.0 mm long for *B. s. siamensis* and *B. s. goniomphalos* and 10.5 mm for *B. funiculata*. All three taxa started laying eggs when they were about 18-19 weeks old.

For raising large numbers of *Bithynia* in the laboratory, 12 containers with a total of 360 snails were cultured. A total of 575 eggs were obtained from these cultures. The number of young snails collected after four months was 480, with a mortality rate of 16.5%. It was observed that the most critical period of rearing young snails was during the first two weeks after hatching. Few snails died because of the overgrowth of ostracods or deteriorated mud cultures.

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ECOLOGICAL STUDIES OF LAND SNAILS IN THE HIWASSEE RIVER BASIN OF TENNESSEE, U.S.A.

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ABSTRACT

This study involved preliminary ecological investigations of land snails of the lower Hiwassee River Basin of southeastern Tennessee based on elevation, slope, soil moisture and pH, and forest, microhabitat, and rock type. At least 86 snail species occur within or adjacent to the study area. In this study, 8631 individuals, 28 genera, 57 identified species, and 100 new county distribution records were obtained from 37 stations.

Rock type was a significant factor for 13 species; of these, more were significantly associated with limestone (nine species), as compared with limestone and shale (one species), shale (one species) and dolomite (two species). Other factors (e.g., predation) in the environment may be responsible for the apparent significant association of certain snail species with shale and dolomitic substrata.

Elevation was a significant factor for only seven species. Those species significantly associated with low elevations (two species) probably have high moisture requirements, while those significantly associated with high elevations (five species) may be responding to localized geologic conditions which would tend to result in higher relief.

Slope was an important factor for 15 species. Species significantly associated with moderate and steep slopes (two species) tended to be those which also had an affinity for drier habitats, while species significantly associated with steep and very steep slopes (13 species) also were associated with high soil moisture and later stages of forest succession.

The effects of soil pH and moisture content were determined only for species collected by the one-fourth square meter method. Eight species were significantly associated with soil pH and only six with soil moisture. Species which had an affinity for drier and more acid conditions also tended to be associated with early successional stages on dolomitic substrata. Species which had an affinity for damper and neutral conditions tended to be associated with late successional stages on limestone substrata.

A majority of the snail species were significantly associated with late forest stages (11 species), but only one was significantly associated with early stages. Snails which had an affinity for late successional stages also were associated with neutral soils of high moisture content and steeper slopes. The leaf litter of *Fagus grandifolia* may exert adverse effects on some species of snails.

Microhabitat differences were significantly more important for more species than any other factor (27 species). More species were significantly associated with the leaf litter microhabitat (19 species) than with either log (seven species) or moss (one species) microhabitats. Leaf litter inhabiting species are probably generalized herbivores capable of adapting to a variety of hardwood forests. Species significantly associated with the log microhabitat may exploit the fungi of this microhabitat as a food source.

The presence or absence of snail species is influenced by the interaction of several environmental factors. Congeneric species show different patterns of adaptive coexistence. Some can share the same general habitat by differing in affinities for microhabitat type. Others, which show no obvious difference in microhabitat type, differ dramatically in affinities for physical factors and/or forest type and appear to avoid intrageneric interaction (e.g., competition) by avoiding co-occurrence.

INTRODUCTION

The major intent of this study was to determine the effects of rock type upon the distribution of species of shell-bearing land mollusks (hereafter referred to as snails) in the lower Hiwassee River Basin of southeastern Tennessee, U.S.A. Secondary purposes were to determine

the effects of elevation, slope, and soil, forest, and microhabitat types upon the species, as well as the possible coexistence of common congeneric species. The Hiwassee River Basin was chosen because within a short distance the lower Hiwassee River traverses a majority of the rock formations in the Ridge and Valley Province of eastern Tennessee. The distribution and environmental affinities of snail species provide insight into their autecology.

The region studied (Fig. 1) extended from the mouth of the Hiwassee River southeast to a point 4 mi due west from Oswald Dome. The river begins on the northwestern slopes of the Blue Ridge Mountains in north Georgia and joins the Tennessee River about 35 mi upstream from Chattanooga. It is about 86 mi long and drains an area of 2700 sq mi. Its basin varies in width from about 25 mi near the middle to about 50 mi at each end. The extreme lower end of the river is now part of the Chickamauga Reservoir and has a normal water level of 682 ft elevation. No great floods have been recorded for the Hiwassee River. The Ocoee River, with a watershed of 639 sq mi is the principal tributary in the study area (Tennessee Valley Authority, 1946).

Dickson (1974) reported the following meteorological conditions for the Chattanooga area as recorded at the Lovell Field Weather Bureau Station, which is approximately 30 mi southwest from the center of the study area. Mean annual temperature is 60.0°F and mean annual precipitation is 53.60 in. Mean temperature is 41.6°F in January and 78.3°F in July. The lowest temperature recorded was -10°F (February 1899) and the highest was 106°F (July 1952). The lowest recorded monthly precipitation was 0.04 in (September 1919) and the highest was 15.29 in (April 1911).

Existing detailed geologic maps (Swingle, 1959; Serim, 1965) cover only small portions of the Hiwassee River Basin. Hardeman (1966) covered the study area in a broadly generalized geologic map of the eastern-middle quarter of the State of Tennessee. The stratigraphy of the Ridge and Valley portion of the Hiwassee River Basin was described in detail by Swingle (1959). Geologic formations in the present study were grouped, according to the predominant lithology, into three main categories: shales, dolomites and limestones. The Rome Formation, the undivided Conasauga Group and the Athens Shale are predominantly shales. The Cooper Ridge Dolomite, the Upper Knox Group, the Newala Formation and the Knox Group undivided are predominantly dolomites. The Chickamauga Group undivided, the Holston Formation, the Sequatchie Formation, the Maynardville Limestone and the highly calcareous strata of the Ottosee Formation are predominantly limestones. Other geological formations present in the study area are the Mascot Dolomite, the Lenoir Limestone and the Rockwood Formation; they are poorly exposed and for this reason were not sampled.

The forests of the region lie within the northernmost portion of the Gulf Slope Section of the Oak-Pine Forest Region and just south of the southernmost border of the Oak-Chestnut Forest Region of the Ridge and Valley Section. The study area is bordered to the east by the Southern Appalachian Section of the Oak-Chestnut Forest Region and to the west by the Mixed Mesophytic Forest Region of the Cumberland Plateau (Braun, 1950). Most of the region has been cleared of forests, and those forests which remain have been considerably modified by human activity.

Major industries in the study area include agriculture and manufacturers of chemicals and paper. The paper mill is largely responsible for much of the alteration of the natural vegetation of the region. Pine plantations are numerous and widespread in the Hiwassee River Basin, and clearcutting and bulldozing of tracts of native forests were observed during the course of this study. *Pinus* species not native to the study area occasionally were encountered in native forests and are intepreted as escaped from pine plantations.

The principal zoogeographic works that pertain to the area under study are by Binney (1873), Archer (1939b), Burch (1969) and Te (1976). The study area lies within the Appalachian Valley subprovince of the Cumberlandian province in the subtropical Allegheny subregion within the East American Division, but contains elements of both Interior and Austroriparian provinces. Archer (1939b) stated that the snail fauna of the Appalachian Valley

FIG. 1. Location of all investigated stations in the Hiwassee River Basin of southeastern Tennessee.

lacks endemic species and is somewhat similar to that of the Cumberland Plateau subprovince. Hubricht (1962, 1977) has described three species which may be endemic to the Appalachian Valley subprovince in Tennessee.

Very little is known about the ecology of many species of snails which occur in the Cumberlandian province. With the exception of the works of Burch (1955, 1956) and Getz (1974), most field studies of North American snails have consisted of little environmental analysis but rather contain much of the isolated, detailed observations of naturalists. Boycott (1934) observed that distribution was influenced by the life history of a given species. The most critical factors influencing the distribution of snails are thought to be the availability of calcium, moisture, food and shelter (Newell, 1967; Evans, 1972). Evans (1972) also listed climate, physical and chemical properties of the soil and ground surface, vegetation structure, lack of disturbance, and parasites as important factors. Karlin (1961) and Blinn (1963) were of the opinion that light has no effect on the activity of those species they investigated.

METHODS

The 37 sampling stations were located within naturally occurring forests on geologic strata traversed by the Hiwassee River. In order to reduce the number of variables, all collections were made on north facing slopes. For each rock formation sampled, stations were selected to represent, as equally as possible, both the north and south sides of the Hiwassee River. With the exception of soil work, sampling was conducted from late May to early June, 1979.

The forest at each station was sampled by the Bitterlich method as described by Grosenbaugh (1952) and Dilworth & Bell (1977). The trees sampled at each station were selected with a tube-type Bitterlich angle gauge using a Basal Area Factor of ten. The diameters were measured to the nearest inch at breast height. Heights of the canopy layers of vegetation (T_1 the top, T_2 the intermediate, and T_3 the lowest tree layer) were measured with the clinometer and range finder. Ten samples, approximately 100 ft apart, were taken in each stand. Relative frequency, relative dominance, stem density and basal area for each stand were calculated using the method described by Dilworth & Bell (1977). Relative frequency, relative dominance and stem density were summed to obtain an Importance Value (I.V.) for each tree species sampled at each station, as described by Curtis & MacIntosh (1951). The approximate successional stage of each forest stand was identified on the basis of I.V. and by the use of indicator species. Nomenclature of the trees follows that of Harlow & Harrar (1969).

Slope azimuth was measured with a compass, slope angle with a clinometer and elevation with an altimeter.

Four methods were employed in sampling the snails at each station. The first sampled the leaf litter and A-1 horizon and involved the use of a metal frame consisting of four aluminum shafts 50 cm in length, which could be assembled to form a square plot with an area of ¼ sq m. At each station, the plot was well inside the forest boundaries and on terrain and leaf litter cover typical of the general forest floor. The sample plot was excavated by trowel until all leaf litter, humus and soil in the A-1 horizon had been removed and placed on a ½-in mesh steel screen suspended over a 5-gal bucket to remove the larger sticks, leaves and rocks. The material remaining on the screen carefully was examined for large snail shells. The material which fell into the bucket was transferred to large plastic sacks for temporary storage.

The second method was used to sample a single large log at each station and involved taking 1 liter of debris from the log/soil interface. A piece of wood was taken from each log sampled and identified to genus and, when preservation permitted, to species.

The third method was employed to sample snails in mosses. One liter of moss was collected from only one location at each station and carefully placed in containers so nothing was lost. The mosses were determined by David K. Smith, Department of Botany, University of Tennessee, Knoxville. Nomenclature of mosses follows Crum et al. (1973).

The fourth method was a 15-min search of the station area for larger snails that characteristically occur at lower densities in the environment. All likely habitats, including logs, flat slabs of stone and leaf-filled surface depressions, were examined. Snails collected alive were killed by drowning and were transferred to 70% ethyl alcohol for preservation.

The stations were revisited in early October 1979 to collect soil samples for the analysis of soil pH and soil moisture. All of the soil samples were taken during a 48-hr period during which no rain fell. Soil samples were taken by pressing a tin canister into the A-1 soil horizon after the area had been cleared of leaf litter and humus. Four samples were taken at each station, one from each side of the ¼ sq m sample plot. The four subsamples were combined and stored in a plastic bag on ice until soil analyses could be

performed. Skin contact with soil samples was avoided at all times and fresh tin canisters were utilized at each station to insure contamination-free samples. Field and oven-dried weights were determined and percent moisture was calculated for each soil sample following standard methods described by Lutz & Chandler (1946). Prior to the pH determination, soil samples were allowed to reach room temperature (28°C) over a 24-hr period and moistened to a thick paste with distilled water. Determinations of pH were made with a Fisher Accumet Model 120 pH meter which had been standardized with Fisher Buffer of pH 7.0.

Snail shells were recovered from sample material by flotation in water, followed by drying the supernatant in an oven until completely dry. This was followed by a second flotation of the remaining debris and shells in xylene as described by Coney et al. (1981). The supernatant was then hand sorted for snail shells under magnification.

Snails were identified with the aid of Pilsbry's *Land Mollusca of North America* (1940, 1946, 1948) and with a synoptic collection of 177 species of snails borrowed from the Mollusk Division, Museum of Zoology, The University of Michigan. All individuals of taxonomically difficult genera (i.e., *Paravitrea, Glyphyalinia* and *Mesomphix*) were sent to Leslie Hubricht, Meridian, Mississippi, for determination.

The writers combined immature individuals of Pupillidae and Succineidae into the taxon "immature spp.". *Punctum* specimens could be determined to species based on shell characters provided the shell diameter was greater than 0.7 mm. Very young shells having a diameter of less than 0.7 mm were combined as the taxon *Punctum* spp. Finally, some immature individuals were not identifiable to family with certainty, due to the absence of key shell characteristics. In this study, they were placed in the category "unidentified immatures". All specimens found during this study were deposited with the Department of Biological Sciences, East Tennessee State University.

For statistical analyses, the total range of each environmental factor measured was divided into three specific ranges (e.g., elevation: low, 740-820 ft; medium, 840-920 ft; high, 940-1120 ft), based either on natural breaks in the total range or on arbitrarily imposed limits. For statistical analyses of elevation, slope, and forest and rock types, the results of the four sampling methods at each station were combined, since environmental factors, rather than microhabitat differences, were presumed to influence the presence or absence of snail species at any given station. Statistical analyses of the effects of soil moisture and pH upon snails were based only on the results of the ¼ sq m samples, while the effect of microhabitat type on snails was based on statistical analysis of the leaf litter, log and moss sampling methods. Analyses of ecological factors studied were performed on each of 57 snail species using the R x C Test of Independence with the G-Test as described by Sokal & Rolf (1969). Results of these analyses were inconclusive for species present at less than four stations. This test detects significant associations using presence/absence data from which percent presence was also calculated and used to determine environmental affinities for each of the 57 species. Interpretation of significant values was based upon the percent presence observed; however, differences of less than 6% were considered to be statistically equivalent. Statements concerning the affinity of snail species for environmental factors are based on highest relative frequency (i.e., percent presence). Correlations of snail species with environmental factors showed subjective trends and were based upon increasing or decreasing percent presence. Congeneric species were compared using a Chi-square 2 x 2 contingency table (Krebs, 1972) to test the null hypothesis that any two congeneric species (each present at a minimum of four stations) were not associated. Coefficients of association (V) (Krebs, 1972) also were calculated. Interpretations of the extent and direction of association of congeneric species were aided by comparisons of certain of their environmental affinities.

RESULTS

A variety of environmental factors was chosen for study at each of the 37 stations. A description of geographic and physical factors studied and/or recorded at each station is given by county, topographic quadrangle, rock type, geologic substrata, azimuth of North, elevation, slope, soil moisture and soil pH (Table 1). A description of biotic factors studied and/or recorded at each station is given by forest successional stage, basal area, canopy height, taxa of log and moss samples, and moss substrate (Table 2).

The number of individuals collected by each sampling method is given for each species (Table 3). Also given in this table is the relative abundance of each identified species as percent composition, based upon the total number of snails collected (8631). In addition, the total number of stations is given for each species and is referred to as total frequency.

Each species was tested for statistically significant associations with elevation, slope, soil moisture and soil pH, and forest, microhabitat and rock types. Correlations and affinities of species with the above factors were based upon percent presence values. The mean was

TABLE 1. Data on physical factors at stations.

Station	County	Topographic quadrangle	Rock type	Geologic substrata	Azimuth of North	Elevation[1]	Slope gradient as %	Soil moisture as %	Soil pH
1	Polk	Benton	Dolomite	Knox Group	0°	840	18	16.7	5.4
2	Bradley	Benton	Dolomite	Copper Ridge Dolomite	0°	860	20	19.0	5.7
3	Bradley	Benton	Limestone	Holston Formation	31-0°	820	45	23.0	4.6
4	Bradley	Benton	Shale	Athens Shale	0°	820	40	26.6	6.5
5	Bradley	Benton	Dolomite	Upper Knox Group	0°	840	35	15.1	5.2
6	Bradley	East Cleveland	Dolomite	Copper Ridge Dolomite	170°	840	25	22.3	5.8
7	Bradley	Charleston	Shale	Rome Formation	70°	760	50	20.0	5.6
8	Bradley	Charleston	Limestone	Maynardville Limestone	125°	740	40	27.9	6.7
9	Bradley	Charleston	Dolomite	Knox Group	0°	840	25	19.0	4.9
10	McMinn	Etowah	Dolomite	Knox Group	6°	940	20	20.1	6.4
11	Bradley	Benton	Shale	Lower Conasauga	5°	760	70	–[2]	5.2
12	Bradley	Birchwood	Shale	Rome Formation	0°	780	45	12.8	4.7
13	Bradley	Birchwood	Limestone	Sequatchie Formation	0°	1120	65	21.0	6.2
14	Bradley	Birchwood	Limestone	Sequatchie Formation	25°	1020	65	33.0	6.6
15	Meigs	Birchwood	Limestone	Sequatchie Formation	0°	940	40	23.8	6.0
16	Meigs	Birchwood	Limestone	Chickamauga Group	0°	800	15	23.6	6.6
17	Meigs	Birchwood	Dolomite	Knox Group	340-0°	880	15	17.5	6.0

18	Meigs	Big Spring	Dolomite	Newala Formation	325°	740	20	15.7	5.5
19	Meigs	Big Spring	Dolomite	Knox Group	0°	800	57	19.2	5.6
20	Meigs	Decatur	Limestone	Sequatchie Formation	0-30°	960	40	–[2]	–[2]
21	Meigs	Decatur	Limestone	Sequatchie Formation	13°	820	50	–[2]	–[2]
22	Meigs	Big Spring	Dolomite	Newala Formation	270-10°	800	30	16.1	5.3
23	Meigs	Birchwood	Dolomite	Knox Group	0-30°	800	30	21.4	5.6
24	Meigs	Birchwood	Limestone	Sequatchie Formation	350°	840	85	28.2	6.7
25	Meigs	Big Spring	Limestone	Chickamauga Group	50°	740	20	16.3	4.5
26	Polk	Benton	Shale	Lower Conasauga	90-270°	840	30	–[2]	5.6
27	McMinn	Calhoun	Dolomite	Copper Ridge Dolomite	90-270°	900	20	15.5	5.2
28	McMinn	Calhoun	Limestone	Holston Formation	45-300°	940	60	17.8	6.4
29	McMinn	Calhoun	Dolomite	Copper Ridge Dolomite	0°	840	30	20.9	5.1
30	McMinn	Charleston	Dolomite	Knox Group	0°	920	30	23.6	6.0
31	McMinn	Goodfield	Shale	Rome Formation	85°	880	15	17.1	5.0
32	Meigs	Goodfield	Shale	Rome Formation	0°	980	50	20.0	5.9
33	Meigs	Goodfield	Limestone	Maynardville Limestone	290°	880	50	22.3	6.5
34	McMinn	Calhoun	Shale	Athens Shale	30-0-330°	900	20	22.3	5.5
35	McMinn	Calhoun	Dolomite	Upper Knox Group	30-0-330°	900	20	22.2	5.2
36	McMinn	Calhoun	Limestone	Ottosee Formation	10°	740	30+	31.3	7.1
37	McMinn	Calhoun	Limestone	Maynardville Limestone	0-25°	800	35	30.3	6.8

[1] Measured as feet above sea level.

[2] Data unavailable.

TABLE 2. Data on biotic factors at stations.

Station	Forest data					Taxa of logs sampled for 1 liter of log debris	Taxa of moss sampled for 1 liter of moss	Moss substrata
	Successional stage	Basal area[1]	Canopy height[2]					
			T_1	T_2	T_3			
1	Oak-Pine	76.5	71	30	0	*Castanea dentata*	*Hypnum fertile*	Decorticated log
2	Oak-Poplar	82.6	101	20	1	*Castanea dentata*	*Leucobryum albidum*	Decorticated log
3	Disturbed Oak-Hickory	84.7	84	–[3]	–[3]	*Castanea dentata*	*Anomodon rostratus*	Bedrock
4	Disturbed Oak-Hickory-Cedar	62.1	85	30	0	*Lepidobalanus* group	*Platygyrium repens*	Decorticated log
5	Oak-Pine	64.7	104	41	0	*Carya* sp.	*Bryoandersonia illecebra* *Aulacomnium heterostichum*	Ground surface
6	Oak-Pine	54.6	90	42	0	*Lepidobalanus* group	*Anomodon attenuatus*	*Quercus prinus*[4]
7	Oak-Pine	57.0	73	58	22	*Liriodendron tulipifera*	*Anomodon attenuatus*	*Quercus alba*[4]
8	Disturbed Oak-Hickory	40.0	78	39	20	*Lepidobalanus* group	*Anomodon attenuatus* *Bryoandersonia illecebra*	Bedrock
9	Oak-Pine	58.7	96	66	35	*Carya* sp.	*Anomodon attenuatus*	*Quercus alba*[4]
10	Oak-Pine	58.1	104	52	18	*Castanea dentata*	*Dicranum scoparium*	Decorticated log
11	Oak-Hickory-Sugar Maple	72.0	130	75	35	*Erythrobalanus* group	*Aulacomnium heterostichum* *Bartramia pomiformis*	Ground surface
12	Oak-Pine	56.7	95	81	50	*Carya* sp.	*Dicranum scoparium*	Ground surface
13	Mixed Mesic	58.3	88	30	0	*Aesculus octandra*	*Mnium affine* var. *ciliare* *Anomodon rostratus*	Bedrock
14	Mixed Mesic	56.4	99	30	0	*Castanea dentata*	*Hygroamblystegium tenex*	Bedrock
15	Oak-Hickory-Sugar Maple	73.4	114	83	20	*Erythrobalanus* group	*Eurhynchium hians* *Anomodon attenuatus*	Bedrock
16	Oak-Cedar	70.7	66	45	23	*Erythrobalanus* group	*Anomodon attenuatus*	*Quercus stellata*[4]
17	Disturbed Oak-Hickory-Pine	62.6	87	30	10	*Prunus avium*	*Bryoandersonia illecebra*	Ground surface

18	Oak-Hickory-Red Maple	84.5	110	50	30	*Lepidobalanus* group	*Hypnum fertile*	Decorticated log
19	Oak-Hickory-Red Maple	82.8	85	50	25	*Erythrobalanus* group	*Leucobryum albidum*	Decorticated log
20	Oak-Hickory-Sugar Maple	87.5	_[3]	_[3]	_[3]	*Castanea dentata*	*Aulacomnium heterostichum*	*Carya tomentosa*[4]
							Anomodon rostratus	
21	Oak-Hickory-Sugar Maple	77.0	120	40	0	*Liriodendron tulipifera*	*Bryoandersonia illecebra*	Bedrock
22	Oak-Pine	85.0	95	40	20	*Lepidobalanus* group	*Anomodon rostratus*	*Nyssa sylvatica*[4]
23	Oak-Hickory-Red Maple	89.3	98	68	20	*Carya* sp.	*Leucobryum albidum*	Decorticated log
							Dicranum scoparium	
24	Oak-Hickory-Sugar Maple	68.8	_[3]	_[3]	_[3]	*Erythrobalanus* group	*Hygroamblystegium tenax*	Bedrock
25	Oak-Cedar	104.0	75	40	20	*Lepidobalanus* group	*Bryoandersonia illecebra*	*Quercus falcata*[4]
26	Oak-Hickory-Red Maple	96.6	105	46	20	*Lepidobalanus* group	*Thuidium delicatulum*	*Quercus alba*[4]
27	Oak-Hickory-Red Maple	85.7	95	75	30	*Erythrobalanus* group	*Anomodon rostratus*	*Acer rubrum*[4]
28	Oak-Poplar	146.2	150	65	30	*Castanea dentata*	*Fissidens taxifolius*	Bedrock
29	Oak-Hickory-Red Maple	106.0	150	64	46	*Lepidobalanus* group	*Anomodon attenuatus*	Ground surface
							Bryoandersonia illecebra	
							Campylium chrysophyllum	
30	Oak-Pine	88.2	98	56	20	*Erythrobalanus* group	*Dicranum scoparium*	Ground surface
31	Oak-Pine	113.5	106	84	35	*Lepidobalanus* group	*Leucobryum albidum*	Ground surface
32	Oak-Hickory-Red Maple	97.8	112	70	25	*Lepidobalanus* group	*Bryoandersonia illecebra*	*Quercus prinus*[4]
33	Disturbed Oak-Hickory-Cedar	82.9	83	55	20	*Erythrobalanus* group	*Anomodon rostratus*	Bedrock
34	Disturbed Oak-Hickory	74.5	145	44	25	*Lepidobalanus* group	*Anomodon rostratus*	*Quercus alba*[4]
35	Oak-Pine	101.0	84	40	25	*Erythrobalanus* group	*Bryoandersonia illecebra*	*Quercus falcata*[4]
36	Oak-Hickory-Cedar	114.4	80	64	30	*Castanea dentata*	*Thuidium delicatulum*	Bedrock
37	Disturbed Oak-Hickory-Cedar	113.4	120	69	30	*Castanea dentata*	*Bryoandersonia illecebra*	Bedrock

[1]Measured as feet per square acre.

[2]Measured in feet.

[3]Data unavailable.

[4]Moss collected from trunk of living tree.

TABLE 3. Number of individuals by sampling method, percent composition and total station frequency of snails.

Species[1]	No. individuals by sampling method				Total	%[2]	Total frequency
	¼ sq m	Liter of moss	Liter of log debris	15 min search			
Striatura meridionalis	1355	64	105	0	1524	17.7	37
Punctum minutissium	1327	23	41	0	1391	16.1	34
Gastrocopta pentodon	524	12	7	0	543	6.3	15
Glyphyalinia indentata	427	8	40	3	478	5.5	33
Ventridens gularis	277	4	28	61	370	4.3	19
Carychium exile	343	1	13	0	357	4.1	9
Guppya sterkii	277	30	33	0	340	3.9	23
Gastrodonta interna	21	2	220	61	304	3.5	22
Glyphyalinia wheatleyi	266	0	19	0	285	3.3	24
Mesodon inflectus	46	0	65	131	242	2.8	33
Vertigo gouldi	4	202	0	0	206	2.4	9
Zonitoides arboreus	11	2	175	15	203	2.4	25
Punctum smithi	162	3	4	0	169	2.0	10
Discus patulus	86	1	17	33	137	1.6	8
Hawaiia minuscula	108	15	6	0	129	1.5	27
Euconulus chersinus	85	2	1	0	88	1.0	15
Ventridens intertextus	40	0	6	21	67	0.8	9
Pomatiopsis lapidaria	47	0	4	0	51	0.6	4
Haplotrema concavum	20	0	10	20	50	0.6	11
Glyphyalinia praecox	46	0	0	1	47	0.5	5
Stenotrema stenotrema	7	0	8	30	45	0.5	18
Ventridens collisella	35	0	0	9	44	0.5	5
Punctum vitreum	43	0	0	0	43	0.5	2
Helicodiscus notius	29	0	12	0	41	0.5	8
Vertigo parvula	33	4	2	0	39	0.5	8
Strobilops texasiana	36	0	2	0	38	0.4	5
Euconulus dentatus	30	0	7	0	37	0.4	4
Mesodon perigraptus	0	0	6	28	34	0.4	13
Paravitrea variabilis	24	0	10	0	34	0.4	2
Gastrocopta contracta	8	0	25	0	33	0.4	6
Strobilops aenea	2	5	25	0	32	0.4	7
Mesomphix perlaevis	20	0	0	10	30	0.3	2
Mesomphix latior	19	0	1	9	29	0.3	2
Carychium nannodes	0	1	26	0	27	0.3	1
Mesodon rugeli	1	0	5	20	26	0.3	3
Anguispira strongylodes	4	1	4	16	25	0.3	6
Mesodon zaletus	3	1	0	16	20	0.2	4
Triodopsis vulgata	1	0	1	17	19	0.2	5
Polygyra plicata	16	0	0	2	18	0.2	7
Ventridens lasmodon	16	0	0	2	18	0.2	1
Cionella morseana	16	0	1	0	17	0.2	2
Glyphyalinia sculptillis	0	0	13	2	15	0.2	3
Ventridens elliotti	0	0	5	10	15	0.2	2
Mesodon thyroidus	0	0	0	11	11	0.1	6
Columella simplex	9	0	1	0	10	0.1	2
Helicodiscus hadenoecus	8	0	1	0	9	0.1	1
Triodopsis tridentata	0	0	0	9	9	0.1	1
Stenotrema hirsutum	5	0	0	3	8	0.1	3
Glyphyalinia cumberlandiana	0	0	8	0	8	0.1	2
Triodopsis alabamensis	5	0	0	3	8	0.1	1
Mesomphix capnodes	3	0	0	1	4	–[3]	1
Triodopsis albolabris	0	0	0	4	4	–[3]	1
Gastrocopta corticaria	0	3	0	0	3	–[3]	2
Mesodon elevatus	0	0	0	3	3	–[3]	1
Triodopsis caroliniensis	0	0	0	3	3	–[3]	1
Ventridens pilsbryi	2	0	0	0	2	–[3]	1
Gastrocopta armifera	1	0	0	0	1	–[3]	1
Total	5848	384	957	554	7743		

[1] Immature undetermined species omitted.
[2] Based on total number of land mollusks = 8631.
[3] Less than 0.1%.

calculated for each specific range of a given factor by dividing the total number of species present by the total number of stations.

Rock type

As shown in Table 4, 13 species were significantly associated with one or more rock types. Thirty-four species ($\bar{x} = 4.3$) were found at stations (N = 8) underlain by shale substrata, and one species was significantly associated with this rock type. Thirty-six species ($\bar{x} = 2.4$) were found at stations (N = 15) underlain by dolomitic substrata, and two species were significantly associated with this rock type. Forty-nine species ($\bar{x} = 3.5$) were found at stations (N = 14) underlain by limestone substrata, and nine species were significantly associated with this rock type. One species was significantly associated with both limestone and shale rock types. Eight species showed no difference in presence or absence due to rock type.

Glyphyalinia cumberlandiana was significantly associated with shale substrata, and *Glyphyalinia indentata, Gastrodonta interna* and *Ventridens gularis* had a high affinity for this rock type. *Hawaiia minuscula* and *Ventridens intertextus* were significantly associated with dolomitic substrata, and *Strobilops aenea* and *Punctum smithi* had a high affinity for this rock type. *Carychium exile, Vertigo parvula, Vertigo gouldi, Anguispira strongylodes, Helicodiscus notius, Euconulus dentatus, Guppya sterkii, Haplotrema concavum* and *Mesodon zaletus* were significantly associated with limestone substrata. *Glyphyalinia wheatleyi* was significantly associated with limestone and shale substrata. *Punctum minutissimum, Punctum vitreum, Glyphyalinia praecox, Ventridens collisella* and *Polygyra plicata* had a high affinity for limestone, whereas *Euconulus chersinus* had a nearly equivalent affinity for limestone and dolomitic substrata.

The importance of calcium accessibility to snails cannot be over-estimated. The shell in most species is composed of aragonite, a crystalline form of calcium carbonate (Evans, 1972). Shell thickness in some species is an almost automatic response to the availability of calcium carbonate (Gould, 1971). Excess calcium carbonate is stored in the shells and may be dissolved during dry periods to buffer carbon dioxide in the blood and thus prevent asphyxiation (Baker, 1958). Burch (1955) determined that the distribution of snails in eastern Virginia was limited largely by the amount of calcium, magnesium and organic matter in the soil. These validate the fact that the zoogeography of land snails is subject to their physiological adaptability to environmental selection pressures.

The calcium carbonate content of the geological formations in the study area ranges from 0.06% to 100% (taken from Maher & Milici, 1975, unless otherwise stated) and is as follows: Rome Formation, 0.06% (Whittimore, pers. comm.); Conasauga Group, approximately 50-90%; Athens Shale, 0.35-14.63% (Whittimore, pers. comm.); Lower and Middle Knox Group (includes Copper Ridge Dolomite), approximately 50-60%; Upper Knox Group (includes Newala Formation), approximately 50-75%; Chicamauga Group, approximately 60-98%; Holston Formation, approximately 95-100%; Maynardville Limestone, approximately 80-95%. No information was found on the calcium carbonate content of the Sequatchie and Ottosee Formations.

Geologically different calcareous strata have produced calcium concentrations in the soil which are roughly proportional to their texture and solubility. Shales in the study area are very low in calcium carbonate and are softer than limestones and dolomites and weather at a much faster rate. For this reason, the calcium resulting from shales might equal that of limestones if rapid erosion of shales did not occur. Soils derived from dolomitic strata may be very low in calcium and may be very poor in snails.

Elevation

Only seven species were significantly associated with one or more elevation ranges (Table 4). Fifty species ($\bar{x} = 3.3$) were found at low elevations (740-820 ft, 15 stations); of these,

TABLE 4. Percent presence and G-test values of snails for physical factors.

Species	Rock type				Elevation				Slope			
	Shales (N=8)	Dolomites (N=15)	Limestones (N=14)	G value (df=2)	740-820′ (N=15)	840-920′ (N=15)	940-1120′ (N=7)	G value (df=2)	15-30% (N=18)	35-57% (N=14)	60-85% (N=5)	G value (df=2)
Carychium exile	25.0	0.0	50.0	12.649**	33.3	6.7	42.9	5.050	0.0	35.7	80.0	17.801**
Carychium nannodes	0.0	0.0	7.1	1.990	6.7	0.0	0.0	1.847	0.0	7.1	0.0	1.990
Cionella morseana	0.0	0.0	14.3	4.078	0.0	6.7	14.3	2.471	0.0	7.1	20.0	3.352
Gastrocopta armifera	12.5	0.0	0.0	3.166	6.7	0.0	0.0	1.847	0.0	7.1	0.0	1.990
Gastrocopta contracta	12.5	13.3	21.4	0.443	6.7	13.3	42.9	4.111	11.1	7.1	60.0	6.307*
Gastrocopta pentodon	12.5	46.7	50.0	3.796	60.0	20.0	42.9	5.197	44.4	42.9	0.0	6.109*
Gastrocopta corticaria	0.0	6.7	7.1	1.008	6.7	6.7	0.0	0.865	11.1	0.0	0.0	3.003
Vertigo parvula	0.0	6.7	50.0	11.878**	40.0	13.3	0.0	6.663*	11.1	42.9	0.0	6.954*
Vertigo gouldi	12.5	6.7	50.0	8.270*	26.7	20.0	28.6	0.269	5.6	42.9	40.0	7.479*
Columella simplex	0.0	6.7	7.1	1.008	6.7	6.7	0.0	0.865	5.6	7.1	0.0	0.632
Strobilops texasiana	25.0	13.3	7.1	1.324	6.7	20.0	14.3	1.205	16.7	14.3	0.0	1.603
Strobilops aenea	12.5	26.7	14.3	0.984	20.0	13.3	28.6	0.725	27.8	14.3	0.0	3.140
Anguispira strongylodes	0.0	0.0	42.9	13.678**	20.0	0.0	42.9	8.227*	0.0	28.6	40.0	9.318**
Discus patulus	25.0	13.3	28.6	1.105	26.7	6.7	42.9	4.328	5.6	35.7	40.0	5.930
Helicodiscus notius	25.0	0.0	42.9	10.515**	20.0	20.0	28.6	0.234	11.1	28.6	40.0	2.594
Helicodiscus hadenoecus	0.0	6.7	0.0	1.847	6.7	0.0	0.0	1.847	5.6	0.0	0.0	1.470
Punctum minutissimum	75.0	93.3	100.0	4.478	86.7	93.3	100.0	1.696	88.9	92.9	100.0	1.061
Punctum vitreum	0.0	0.0	14.3	4.078	0.0	0.0	28.6	7.185*	0.0	0.0	40.0	8.831*
Punctum smithi	25.0	33.3	21.4	0.540	33.3	26.7	14.3	0.947	27.8	28.6	20.0	0.155
Glyphyalinia cumberlandiana	25.0	0.0	0.0	6.564*	6.7	0.0	14.3	2.471	0.0	7.1	20.0	3.352
Glyphyalinia wheatleyi	87.5	33.3	85.7	11.366**	60.0	60.0	85.7	1.850	44.4	85.7	80.0	6.755*
Glyphyalinia indentata	100.0	86.7	85.7	2.085	93.3	86.7	85.7	0.478	94.4	85.7	80.0	1.137
Glyphyalinia praecox	0.0	6.7	28.6	5.207	20.0	6.7	14.3	1.205	5.6	21.4	20.0	2.030
Glyphyalinia sculptillis	25.0	6.7	0.0	4.478	6.7	13.3	0.0	1.696	11.1	0.0	20.0	3.262
Mesomphix perlaevis	0.0	0.0	14.3	4.078	0.0	0.0	28.6	7.185*	0.0	7.1	20.0	3.352

Mesomphix latior	0.0	13.3	0.0	3.781	0.0	13.3	0.0	3.781	11.1	0.0	0.0	3.003
Mesomphix capnodes	0.0	0.0	7.1	1.990	6.7	0.0	0.0	1.847	5.6	0.0	0.0	1.470
Paravitrea variabilis	12.5	0.0	7.1	2.328	13.3	0.0	0.0	3.781	0.0	14.3	0.0	4.078
Hawaiia minuscula	37.5	86.7	78.6	6.268*	60.0	80.0	85.7	2.237	77.8	64.3	80.0	0.858
Euconulus chersinus	25.0	46.7	42.9	1.114	46.7	40.0	28.6	0.667	50.0	28.6	40.0	1.526
Euconulus dentatus	0.0	0.0	28.6	8.597*	6.7	0.0	42.9	8.439*	5.6	0.0	60.0	10.894**
Guppya sterkii	26.5	40.0	85.7	6.823*	60.0	53.3	85.7	2.422	44.4	71.4	100.0	7.599*
Gastrodonta interna	75.0	60.0	50.0	1.365	46.7	66.7	71.4	1.762	61.1	57.1	60.0	0.052
Ventridens collisella	0.0	6.7	28.6	5.207	13.3	0.0	42.9	7.966*	0.0	14.3	60.0	11.093**
Ventridens gularis	75.0	40.0	57.1	2.740	53.3	60.0	42.9	0.571	55.6	64.3	20.0	3.066
Ventridens lasmodon	0.0	6.7	0.0	1.847	0.0	6.7	0.0	1.847	5.6	0.0	0.0	1.470
Ventridens pilsbryi	0.0	6.7	0.0	1.847	6.7	0.0	0.0	1.847	0.0	7.1	0.0	1.990
Ventridens intertextus	12.5	46.7	7.1	7.093*	40.0	20.0	0.0	5.852	38.9	14.3	0.0	5.514
Ventridens elliotti	12.5	6.7	0.0	2.185	0.0	13.3	0.0	3.781	11.1	0.0	0.0	3.003
Zonitoides arboreus	62.5	66.7	71.4	0.194	60.0	66.7	85.7	1.599	66.7	64.3	100.0	3.870
Striatura meridionalis	100.0	100.0	100.0	0.000	100.0	100.0	100.0	0.000	100.0	100.0	100.0	0.000
Haplotrema concavum	37.5	0.0	57.1	15.327**	33.3	13.3	57.1	4.597	5.6	42.9	80.0	13.184**
Polygyra plicata	12.5	6.7	35.7	4.268	20.0	6.7	42.9	3.973	5.6	21.4	60.0	6.891*
Stenotrema hirsutum	25.0	0.0	7.1	4.621	6.7	6.7	14.3	0.386	11.1	7.1	0.0	1.061
Stenotrema stenotrema	25.0	53.3	57.1	2.419	40.0	46.7	71.4	1.972	33.3	71.4	40.0	4.870
Mesodon thyroidus	12.5	20.0	14.3	0.276	13.3	26.7	0.0	3.622	27.8	7.1	0.0	4.324
Mesodon zaletus	0.0	0.0	28.6	8.597*	6.7	6.7	28.6	2.276	0.0	7.1	60.0	11.413**
Mesodon elevatus	0.0	0.0	7.1	1.990	6.7	0.0	0.0	1.847	0.0	7.1	0.0	1.990
Mesodon perigraptus	50.0	40.0	21.4	2.144	33.3	40.0	28.6	0.311	33.3	35.7	40.0	0.079
Mesodon inflectus	100.0	86.7	86.7	2.085	93.3	80.0	100.0	2.988	88.9	92.9	80.0	0.581
Mesodon rugeli	0.0	13.3	7.1	1.839	6.7	13.3	0.0	1.696	11.1	7.1	0.0	1.061
Triodopsis vulgata	12.5	6.7	21.4	1.382	6.7	6.7	42.9	5.050	5.6	7.1	60.0	7.647*
Triodopsis alabamensis	0.0	0.0	7.1	1.990	6.7	0.0	0.0	1.847	5.6	0.0	0.0	1.470
Triodopsis tridentata	0.0	0.0	7.1	1.990	6.7	0.0	0.0	1.847	0.0	7.1	0.0	1.990
Triodopsis caroliniensis	0.0	0.0	7.1	1.990	0.0	0.0	14.3	3.453	0.0	0.0	20.0	4.191
Triodopsis albolabris	0.0	0.0	7.1	1.990	6.7	0.0	0.0	1.847	5.6	0.0	0.0	1.470
Pomatiopsis lapidaria	12.5	0.0	21.4	4.772	26.7	0.0	0.0	7.951*	0.0	21.4	20.0	5.796

*Significant P< .05

**Significant P< .01

only two were significantly associated with this range. Thirty-nine species ($\bar{x} = 2.6$) were found at medium elevations (840-920 ft, 15 stations), and none were significantly associated with this range. Thirty-six species ($\bar{x} = 5.1$) were found at high elevations (940-1120 ft, seven stations), and five were significantly associated with this range. Eight species were directly correlated and six species were inversely correlated with increasing elevation.

Only *Vertigo parvula* and *Pomatiopsis lapidaria* were significantly associated with low elevations. *Strobilops texasiana, Ventridens gularis* and *Mesodon perigraptus* had a high affinity for medium elevations. *Anguispira strongylodes, Punctum vitreum, Mesomphix perlaevis, Euconulus dentatus* and *Ventridens collisella* were significantly associated with high elevations, and *Strobilops aenea* and *Zonitoides arboreus* had a high affinity for this range. *Gastrocopta contracta, Punctum minutissimum, Glyphyalinia wheatleyi, Hawaiia minuscula, Gastrodonta interna, Stenotrema stenotrema, Mesodon zaletus* and *Triodopsis vulgata* were directly correlated with increasing elevation. *Gastrocopta pentodon, Vertigo parvula, Punctum smithi, Glyphyalinia indentata, Euconulus chersinus* and *Ventridens intertextus* were inversely correlated with increasing elevation.

Slope

Fifteen snail species were significantly associated with one or more slope ranges (Table 4). Forty-one species ($\bar{x} = 2.3$) were found on moderate slopes (15-30%, 18 stations). Forty-five species ($\bar{x} = 3.2$) were found on steep slopes (35-57%, 14 stations), and one species was significantly associated with this range. Thirty-four species ($\bar{x} = 6.8$) were found on very steep slopes (60-85%, five stations), and 11 were significantly associated with this range. In addition, one species was significantly associated with moderate and steep slopes and two with steep and very steep slopes. Nine species were directly correlated and five species were inversely correlated with increasing slope. Four species showed no difference in presence or absence due to slope.

Only *Vertigo parvula* was significantly associated with steep slopes, whereas both *Ventridens gularis* and *Stenotrema stenotrema* had a high affinity for this range. *Carychium exile, Gastrocopta contracta, Anguispira strongylodes, Punctum vitreum, Euconulus dentatus, Guppya sterkii, Ventridens collisella, Haplotrema concavum, Polygyra plicata, Mesodon zaletus* and *Triodopsis vulgata* were significantly associated with very steep slopes, and *Zonitoides arboreus* had a higher affinity for this range. In addition, only *Gastrocopta pentodon* was significantly associated with moderate and steep slopes. *Euconulus dentatus* had an affinity for moderate slopes, and *Strobilops texasiana* and *Punctum smithi* had an affinity for moderate and steep slopes. *Vertigo gouldi* and *Glyphyalinia wheatleyi* were significantly associated with steep and very steep slopes. *Carychium exile, Anguispira strongylodes, Discus patulus, Helicodiscus notius, Punctum minutissimum, Haplotrema concavum, Mesodon zaletus, Mesodon perigraptus* and *Triodopsis vulgata* were directly correlated with increasing slope. *Gastrocopta pentodon, Strobilops aenea, Glyphyalinia indentata, Ventridens intertextus and Mesodon thyroidus* were inversely correlated with increasing slope.

Mowbray & Oosting (1968), Walker et al. (1968) and Losche et al. (1970) observed thinner A horizons as slope angle increased. On steep slopes, soils of the A_1 horizon may erode faster than they develop. Martin (1971) found in the Ridge and Valley Province of east Tennessee that soil pH was directly correlated with steeper slopes. Norton & Smith (1930) believed the most important effect of slope was its influence upon soil moisture and attributed this to an increase in runoff as slope increased. Martin (1971) and Strahler (1978) observed both direct and inverse correlations between different tree species and increasing slope.

Snails are capable of detecting variations in substrate angle as they possess two statocysts which function as gravitational sense organs (Kerkut & Walker, 1975). Theoretically, this mechanism may at least partially explain the rather exclusive occurrence of some species on vertical substrates (e.g., *Gastrocopta corticaria*). In fact, Dillon (1980) found that two species of desert snails differed significantly in their affinity for slope angle.

Soil moisture

In this study only 33 stations could be statistically tested, as two stations were not sampled for soil and two other samples were contaminated. Six snail species were significantly associated with one or more ranges of soil moisture (Table 5). Twenty-two species ($\bar{x} = 2.2$) were found on soils of low moisture content (12.8-17.8%, 10 stations), and no species was significantly associated with this range. Forty-two species ($\bar{x} = 2.5$) were found on soils of medium moisture content (19.0-23.8%, 17 stations), and one species was significantly associated with this range. Thirty-one species ($\bar{x} = 5.2$) were found on soils of high moisture content (26.6-33.0%, six stations), and four species were significantly associated with this range. In addition, one species was significantly associated with medium and high ranges of soil moisture content. Sixteen species were directly correlated and five were inversely correlated with increasing soil moisture content. *Striatura meridionalis* showed no difference in presence or absence due to soil moisture.

Gastrodonta interna was significantly associated with soils of medium moisture content, and *Ventridens gularis* had a high affinity for this range. *Carychium exile, Punctum minutissimum, Guppya sterkii* and *Mesodon inflectus* were significantly associated with high soil moisture content, and *Haplotrema concavum* had a higher affinity for this range. In addition, *Glyphyalinia praecox* was significantly associated with medium and high ranges of soil moisture content, and *Strobilops texasiana* had an affinity for medium and high ranges. *Carychium exile, Vertigo parvula, Vertigo gouldi, Anguispira strongylodes, Discus patulus, Punctum minutissimum, Punctum smithi, Glyphyalinia wheatleyi, Glyphyalinia indentata, Euconulus dentatus, Guppya sterkii, Ventridens collisella, Polygyra plicata, Stenotrema stenotrema, Mesodon zaletus* and *Mesodon inflectus* were directly correlated with increasing soil moisture content. *Gastrocopta pentodon, Strobilops aenea, Helicodiscus notius, Hawaiia minuscula* and *Ventridens intertextus* were inversely correlated with increasing soil moisture content.

Weather and local moisture conditions are closely allied in their effects upon the distribution of all organisms. Moisture is necessary for respiration and reproduction of snails, though some species require more than others. Boycott (1934) and Getz (1974) determined that snail diversity is directly correlated with increasing moisture. Both temperature and rainfall are major factors controlling their activity (Henderson, 1905; Karlin, 1961). Shimek (1930) noted moisture is as important as food in determing distribution, and Baker (1958) believed that snails cannot live without moisture.

Soils with high moisture-retaining capacity, capable of preventing desiccation in summer months, are highly favorable to snails (Evans, 1972). However, Krutzsch (1952) observed that small localized variations in soil moisture and temperature have little influence on snail distribution. Strandine (1941) found that populations of *Succinea ovalis* increased when soil moisture decreased. Excessive soil moisture is known to drown the developing embryos of xeric species (Evans, 1972), and many species are easily drowned if they fall into water, as their mucus becomes so diluted that they cannot crawl out (Boycott, 1934). A variety of structural modifications of the shells of some species is believed to be adaptations to dry habitats (Jacot, 1935; Evans, 1972). Some species are able to inhabit dry environments by confining themselves to more sheltered, moist habitats such as beneath logs and in deep leaf litter (Evans, 1972). When moisture is temporarily in short supply, snails are known to obtain sufficient water from food (Blinn, 1963). Baker (1958) noted that some can exist in a semidormant state for at least as long as five years.

Soil pH

In this study only 35 stations could be statistically tested for effects of soil pH upon snails, since two stations were not sampled for soils. Thirty-nine species ($\bar{x} = 3.6$) were found on neutral soils (pH 6.1-7.1, 11 stations); eight were significantly associated with this range

TABLE 5. Percent presence of snails in relation to soil moisture and pH and G-test values for ¼ square meter samples.

Species	Soil moisture				Soil pH			
	12.8-17.8% (N=10)	19.0-23.8% (N=17)	26.6-33.0% (N=6)	G value (df=2)	4.5-5.3 (N=11)	5.4-6.0 (N=13)	6.1-7.1 (N=11)	G value (df=2)
Carychium exile	0.0	5.9	66.7	12.827**	9.1	0.0	45.5	10.210**
Carychium nannodes	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]
Cionella morseana	0.0	5.9	16.7	2.077	0.0	7.7	9.1	1.579
Gastrocopta armifera	0.0	0.0	16.7	3.556	0.0	0.0	9.1	2.380
Gastrocopta contracta	0.0	11.8	0.0	2.775	0.0	0.0	18.2	4.901
Gastrocopta pentodon	50.0	41.2	33.3	0.451	36.4	38.5	45.5	0.209
Gastrocopta corticaria	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]
Vertigo parvula	10.0	17.6	50.0	3.442	9.1	7.7	45.5	6.117*
Vertigo gouldi	0.0	5.9	33.3	4.861	0.0	0.0	27.3	7.585*
Columella simplex	0.0	5.9	16.7	2.077	0.0	7.7	9.1	1.579
Strobilops texasiana	0.0	17.6	16.7	3.125	9.1	23.1	9.1	1.259
Strobilops aenea	10.0	5.9	0.0	0.982	9.1	7.7	0.0	1.579
Anguispira strongylodes	0.0	5.9	33.3	4.861	0.0	0.0	27.3	7.585*
Discus patulus	10.0	11.8	16.7	0.152	0.0	15.4	18.2	3.283
Helicodiscus notius	10.0	5.9	0.0	0.982	9.1	7.7	0.0	1.579
Helicodiscus hadenoecus	10.0	0.0	0.0	2.461	0.0	7.7	0.0	2.031
Punctum minutissimum	60.0	94.1	100.0	7.005*	63.6	92.3	100.0	7.237*
Punctum vitreum	0.0	5.9	16.7	2.077	0.0	0.0	18.2	4.901
Punctum smithi	0.0	17.6	33.3	4.590	18.2	15.4	18.2	0.046
Glyphyalinia cumberlandiana	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]
Glyphyalinia wheatleyi	40.0	64.7	83.3	3.310	36.4	61.5	81.8	4.936
Glyphyalinia indentata	60.0	82.4	83.3	1.844	54.5	92.3	81.8	4.988
Glyphyalinia praecox	0.0	20.0	16.7	18.213**	18.2	0.0	18.2	4.015
Glyphyalinia sculptillis	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]
Mesomphix perlaevis	10.0	5.9	0.0	0.982	0.0	7.7	9.1	1.579
Mesomphix latior	10.0	0.0	0.0	2.461	0.0	7.7	0.0	2.031

Mesomphix capnodes	0.0	5.9	0.0	1.356	0.0	0.0	9.1	2.380
Paravitrea variabilis	0.0	5.9	16.7	2.077	9.1	0.0	9.1	1.928
Hawaiia minuscula	70.0	70.6	50.0	0.878	81.8	69.2	54.5	1.937
Euconulus chersinus	50.0	23.5	33.3	1.959	54.5	30.8	27.3	2.082
Euconulus dentatus	10.0	11.8	16.7	0.152	0.0	0.0	36.4	10.456**
Guppya sterkii	10.0	58.8	83.3	10.774**	27.3	38.5	81.8	7.846*
Gastrodonta interna	0.0	29.4	0.0	7.475**	9.1	23.1	18.2	0.892
Ventridens collisella	10.0	11.8	33.3	1.617	0.0	7.7	36.4	7.237*
Ventridens gularis	20.0	64.7	33.3	5.754	36.4	69.2	36.4	3.602
Ventridens lasmodon	0.0	5.9	0.0	1.356	9.1	0.0	0.0	2.380
Ventridens pilsbryi	0.0	5.9	0.0	1.356	0.0	7.7	0.0	2.031
Ventridens intertextus	30.0	23.5	0.0	3.338	18.2	30.8	9.1	1.847
Zonitoides arboreus	10.0	23.5	0.0	3.020	9.1	15.4	18.2	0.413
Striatura meridionalis	100.0	100.0	100.0	0.000	100.0	100.0	100.0	0.000
Haplotrema concavum	0.0	11.8	33.3	4.423	9.1	0.0	27.3	5.284
Polygyra plicata	10.0	17.6	33.3	1.309	9.1	15.4	36.4	2.743
Stenotrema hirsutum	0.0	11.8	0.0	2.775	0.0	7.7	9.1	1.579
Stenotrema stenotrema	0.0	11.8	16.7	2.384	0.0	7.7	18.2	2.994
Mesodon thyroidus	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]
Mesodon zaletus	0.0	5.9	16.7	2.077	0.0	0.0	18.2	4.901
Mesodon elevatus	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]
Mesodon perigraptus	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]
Mesodon inflectus	10.0	47.1	66.7	6.604*	27.3	30.8	63.6	3.751
Mesodon rugeli	0.0	5.9	0.0	1.356	0.0	7.7	0.0	2.031
Triodopsis vulgata	0.0	0.0	16.7	3.556	0.0	0.0	9.1	2.380
Triodopsis alabamensis	0.0	5.9	0.0	1.356	0.0	0.0	9.1	2.380
Triodopsis caroliniensis	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]
Triodopsis albolabris	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]	_[1]
Pomatiopsis lapidaria	0.0	5.9	16.7	2.077	18.2	0.0	9.1	3.343

[1]Species absent from tested ¼ sq m samples.

*Significant $P < .05$

**Significant $P < .01$

(Table 5). Thirty species ($\bar{x}$ = 2.3) were found on acid soils (pH 5.4-6.0, 13 stations); no species was significantly associated with this range. Twenty-five species ($\bar{x}$ = 2.3) were found on very acid soils (pH 4.5-5.3, 11 stations); no species was significantly associated with this range. Fourteen species were directly correlated and four were inversely correlated with increasing soil pH. Two species showed no difference in presence or absence due to soil pH.

Carychium exile, Vertigo parvula, Vertigo gouldi, Anguispira strongylodes, Punctum minutissimum, Euconulus dentatus, Guppya sterkii and *Ventridens collisella* were significantly associated with neutral soils, and *Haplotrema concavum* had an affinity for this range. *Strobilops texasiana, Ventridens gularis* and *Ventridens intertextus* had an affinity for acid soils and *Glyphyalinia indentata* and *Gastrodonta interna* for acid and neutral soils. *Gastrocopta pentodon, Vertigo parvula, Vertigo gouldi, Anguispira strongylodes, Discus patulus, Punctum minutissimum, Glyphyalinia wheatleyi, Guppya sterkii, Ventridens collisella, Zonitoides arboreus, Polygyra plicata, Stenotrema stenotrema, Mesodon zaletus* and *Mesodon inflectus* were directly correlated with increasing soil pH. *Strobilops aenea, Helicodiscus notius, Hawaiia minuscula* and *Euconulus chersinus* were inversely correlated with increasing soil pH.

Soil pH is influenced by the underlying geological substrata, amount of soil moisture, and the leaf litter resulting from the local flora (Lutz & Chandler, 1946). The distribution and abundance of snails has been directly correlated with soil pH (Atkins & Lebour, 1923; Strandine, 1941; Cameron, 1973). Boycott (1934) noted that very few individuals were present on very acid soils (pH 5 or less). On very acid soils, snails possess hyaline shells (Atkins & Lebour, 1923), and species diversity and abundance decrease drastically (Cameron, 1973). Burch (1955) found that snails were most frequent on soils of pH 6.3 to 6.7, but did not believe soil pH was a limiting factor.

Forest succession

In this study only 35 stations could be statistically tested for the influence of forest type on snails, as two stations, one a disturbed oak-hickory-pine forest with no snail species and the other an oak-hickory-cedar forest with 20 snail species, could not be tested, since they were singularly different from the other forest types. Twelve species were significantly associated with specific stages of forest succession (Table 6). Although only one species was significantly associated with early stages of forest succession (28 stations), 53 species ($\bar{x}$ = 1.9) were found in these stages. Eleven species were significantly associated with late stages (seven stations); 37 species ($\bar{x}$ = 5.3) were found in these stages. Forty-three species of snails ($\bar{x}$ = 2.0) occurred in forests of the Oak-Pine sere; of these, eight species had a high affinity for this sere. Within the Oak-Pine sere, 33 species ($\bar{x}$ = 3.0) occurred in the oak-pine stage (11 stations), 18 species ($\bar{x}$ = 9.0) in oak-poplar (two stations), and 30 ($\bar{x}$ = 4.2) in oak-hickory-red maple (seven stations). Forty-five species ($\bar{x}$ = 5.0) occurred in forests of the Oak-Cedar sere; of these, seven species had a high affinity for this sere. Within the Oak-Cedar sere, 22 species ($\bar{x}$ = 11.0) occurred in the oak-cedar stage (two stations), 25 species ($\bar{x}$ = 8.3) in disturbed oak-hickory-cedar (three stations), and 24 species ($\bar{x}$ = 8.0) in disturbed oak-hickory (three stations). Within the late stages of forest succession, 33 species ($\bar{x}$ = 6.6) occurred in the oak-hickory-sugar maple stage (five stations), and 23 species ($\bar{x}$ = 11.5) in the mixed mesic stage (two stations). Nine species showed no difference in presence or absence due to forest types.

Gastrocopta pentodon was significantly associated with early stages of forest succession, and eight species had a high affinity for these stages. *Carychium exile, Anguispira strongylodes, Helicodiscus notius, Punctum vitreum, Euconulus dentatus, Guppya sterkii, Ventridens collisella, Haplotrema concavum, Polygyra plicata, Mesodon zaletus* and *Triodopsis vulgata* were significantly associated with late stages of forest succession, and three species had an affinity for these stages.

Shimek (1930) was among the first to note the importance of vegetation with respect to

TABLE 6. Percent presence and G-test values for snails of forest successional stages and microhabitats.

Species	Forest succession									Microhabitat association			
	Oak-pine sere			Late		Oak-cedar sere							
	Oak-pine (N=11)	Oak-poplar (N=2)	Oak-hickory red maple (N=7)	Oak-hickory-sugar maple (N=5)	Mixed mesic (N=2)	Disturbed oak-hickory (N=3)	Disturbed oak-hickory-cedar (N=3)	Oak-cedar (N=2)	G value (df=7)	Leaf litter[1] (N=37)	Moss habitat[2] (N=37)	Log shelter[3] (N=37)	G value (df=2)
Carychium exile	9.1	0.0	0.0	80.0	100.0	0.0	33.3	0.0	22.103†	21.6	2.7	10.8	6.997*
Carychium nannodes	0.0	0.0	0.0	0.0	0.0	33.3	0.0	0.0	5.263	0.0	2.7	2.7	1.640
Cionella morseana	0.0	0.0	0.0	40.0	0.0	0.0	0.0	0.0	8.602	5.4	0.0	2.7	2.828
Gastrocopta armifera	0.0	0.0	0.0	0.0	0.0	0.0	33.3	0.0	5.263	2.7	0.0	0.0	2.215
Gastrocopta contracta	18.2	0.0	0.0	20.0	100.0	0.0	33.3	0.0	12.816	5.4	0.0	13.5	7.373*
Gastrocopta pentodon	27.3	0.0	57.1	40.0	0.0	33.3	100.0	100.0	14.803*	40.5	16.2	16.2	7.604*
Gastrocopta corticaria	9.1	0.0	0.0	0.0	0.0	0.0	0.0	50.0	5.858	0.0	5.4	0.0	4.468
Vertigo parvula	9.1	0.0	0.0	20.0	0.0	66.7	66.7	50.0	12.911	21.6	5.4	5.4	6.289*
Vertigo gouldi	9.1	0.0	0.0	40.0	0.0	33.3	66.7	0.0	11.000	8.1	21.6	0.0	12.271†
Columella simplex	9.1	0.0	0.0	0.0	0.0	0.0	33.3	0.0	4.811	5.4	0.0	2.7	2.828
Strobilops texasiana	18.2	0.0	28.6	0.0	0.0	33.3	0.0	0.0	6.082	13.5	0.0	2.7	8.182*
Strobilops aenea	27.3	0.0	28.6	20.0	0.0	0.0	0.0	50.0	5.985	5.4	2.7	10.8	2.136
Anguispira strongylodes	0.0	0.0	0.0	40.0	100.0	0.0	33.3	0.0	18.159*	8.1	2.7	5.4	1.104
Discus patulus	0.0	0.0	42.9	40.0	50.0	0.0	33.3	0.0	12.146	13.5	2.7	10.8	3.361
Helicodiscus notius	9.1	0.0	0.0	100.0	0.0	0.0	33.3	50.0	24.334†	10.8	0.0	16.2	9.062*
Helicodiscus hadenoecus	0.0	0.0	14.3	0.0	0.0	0.0	0.0	0.0	3.340	2.7	0.0	2.7	1.640

Punctum minutissimum	81.8	100.0	85.7	100.0	100.0	100.0	100.0	100.0	4.303	86.5	37.8	37.8	25.679†
Punctum vitreum	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	15.332*	5.4	0.0	0.0	4.468
Punctum smithi	18.2	50.0	28.6	60.0	0.0	66.7	0.0	0.0	9.750	21.6	5.4	5.4	6.289*
Glyphyalinia cumberlandiana	0.0	0.0	14.3	20.0	0.0	0.0	0.0	0.0	4.587	0.0	0.0	5.4	4.468
Glyphyalinia wheatleyi	45.5	100.0	42.9	80.0	100.0	100.0	100.0	50.0	12.508	64.9	0.0	18.9	47.618†
Glyphyalinia indentata	81.8	100.0	100.0	100.0	50.0	66.7	100.0	100.0	7.854	75.7	10.8	48.6	35.118†
Glyphyalinia praecox	9.1	0.0	0.0	20.0	50.0	66.7	0.0	0.0	10.410	13.5	0.0	0.0	11.466†
Glyphyalinia sculptillis	9.1	0.0	14.3	20.0	0.0	0.0	0.0	0.0	3.028	0.0	0.0	2.7	2.215
Mesomphix perlaevis	0.0	50.0	0.0	20.0	0.0	0.0	0.0	0.0	7.556	5.4	0.0	0.0	4.468
Mesomphix latior	9.1	0.0	14.3	0.0	0.0	0.0	0.0	0.0	2.889	2.7	0.0	2.7	1.640
Mesomphix capnodes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	6.309	2.7	0.0	0.0	2.215
Paravitrea variabilis	0.0	0.0	0.0	0.0	0.0	33.3	33.3	0.0	7.694	5.4	0.0	5.4	3.318
Hawaiia minuscula	63.6	50.0	85.7	100.0	50.0	66.7	33.3	50.0	7.456	70.3	10.8	13.5	38.682†
Euconulus chersinus	36.4	0.0	57.1	60.0	0.0	66.7	0.0	50.0	9.808	37.8	5.4	2.7	21.210†
Euconulus dentatus	0.0	50.0	0.0	0.0	100.0	0.0	0.0	50.0	19.332†	10.8	0.0	2.7	6.230*
Guppya sterkii	27.3	100.0	57.1	100.0	100.0	100.0	66.7	50.0	17.136*	51.4	21.6	27.0	8.226*
Gastrodonta interna	63.6	100.0	57.1	60.0	50.0	100.0	33.3	0.0	9.808	18.9	2.7	54.1	29.247†
Ventridens collisella	0.0	50.0	14.3	0.0	100.0	0.0	0.0	0.0	16.363*	13.5	0.0	0.0	11.466†
Ventridens gularis	36.4	50.0	42.9	80.0	0.0	100.0	100.0	50.0	13.732	48.6	8.1	21.6	16.787†
Ventridens lasmodon	0.0	0.0	14.3	0.0	0.0	0.0	0.0	0.0	3.340	2.7	0.0	0.0	2.215

Ventridens pilsbryi	0.0	0.0	14.3	0.0	0.0	0.0	0.0	0.0	3.340	2.7	0.0	0.0	2.215
Ventridens intertextus	27.3	50.0	42.9	0.0	0.0	0.0	0.0	50.0	9.631	18.9	0.0	10.8	10.487†
Ventridens elliotti	9.1	0.0	14.3	0.0	0.0	0.0	0.0	0.0	2.889	0.0	0.0	2.7	2.215
Zonitoides arboreus	63.6	50.0	71.4	80.0	100.0	66.7	33.3	50.0	4.020	13.5	2.7	59.5	36.923†
Striatura meridionalis	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	0.000	100.0	54.1	48.6	37.564†
Haplotrema concavum	9.1	0.0	0.0	100.0	100.0	33.3	66.7	0.0	29.234†	16.2	0.0	16.2	10.445†
Polygyra plicata	0.0	100.0	0.0	40.0	50.0	33.3	0.0	0.0	18.748†	18.9	0.0	0.0	16.346†
Stenotrema hirsutum	9.1	0.0	14.3	0.0	0.0	0.0	0.0	50.0	5.259	5.4	0.0	0.0	4.468
Stenotrema stenotrema	36.4	50.0	57.1	80.0	50.0	33.3	66.7	0.0	6.323	8.1	0.0	13.5	7.360*
Mesodon thyroidus	0.0	0.0	42.9	0.0	0.0	0.0	33.3	50.0	12.556	0.0	0.0	0.0	–[4]
Mesodon zaletus	0.0	0.0	0.0	40.0	100.0	0.0	0.0	0.0	18.147*	8.1	2.7	0.0	4.422
Mesodon perigraptus	36.4	100.0	57.1	40.0	0.0	66.7	0.0	0.0	12.580	0.0	0.0	13.5	11.466†
Mesodon inflectus	90.9	100.0	100.0	80.0	100.0	100.0	66.7	100.0	4.950	43.2	0.0	51.4	36.489†
Mesodon rugeli	9.1	0.0	14.3	0.0	0.0	0.0	33.3	0.0	4.213	2.7	0.0	5.4	2.828
Triodopsis vulgata	9.1	0.0	0.0	40.0	100.0	0.0	0.0	0.0	15.276*	2.7	0.0	2.7	1.640
Triodopsis alabamensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	6.309	2.7	0.0	0.0	2.215
Triodopsis caroliniensis	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	6.309	0.0	0.0	0.0	–[4]
Triodopsis albolabris	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	6.309	0.0	0.0	0.0	–[4]
Pomatiopsis lapidaria	0.0	0.0	0.0	40.0	0.0	33.3	0.0	0.0	9.926	10.8	0.0	5.4	5.774

[1]¼ sq m samples.
[2]Liter of moss samples.
[3]Liter of log debris samples.
[4]Species found only by timed search method.
*Significant $P < .05$.
†Significant $P < .01$.

distribution of snails. Dillon (1980) found that the presence of vegetational cover was correlated with the presence of two species of desert snails. Boycott (1934) concluded that the presence or absence of any particular plant species did not determine the distribution of any given snail species. Evans (1972) suggested that perhaps the most important factor was the structure of the vegetation and the resultant local temperature and moisture regimes which determined the distribution of snails. However, Burch (1956) gave convincing evidence that snails are very definitely influenced by the dominant tree cover, and Getz (1974) found a direct correlation between tree and snail diversity in the Great Smoky Mountains. Newell (1967) noted that the presence or absence of some snails is due largely to the presence or absence of plant species which can effectively extract calcium from the soil. Jacot (1935) observed that the density of snail species was not correlated with the age of forest stands. However, disturbance is known to cause an impoverishment of the snail fauna whether by forest clearance (Archer, 1939a: Evans, 1972) or by fire (Archer, 1935). Pine usually pioneers in areas underlain by silicious substrata (e.g., dolomites) and cedar in areas underlain by calcareous substrata (e.g., limestones).

Microhabitat

Twenty-seven species were significantly associated with one or more microhabitats (Table 6). Forty-six species ($\bar{x} = 1.2$) occurred in leaf litter (37 stations); of these, 17 species were significantly associated with this microhabitat. Twenty species ($\bar{x} = 0.5$) occurred in moss (37 stations) but only one species was significantly associated with this microhabitat. Thirty-eight species ($\bar{x} = 1.0$) occurred beneath logs (37 stations); seven species were significantly associated with this microhabitat.

Those species significantly associated with the leaf litter microhabitat were *Carychium exile, Gastrocopta pentodon, Vertigo parvula, Strobilops texasiana, Punctum minutissimum, Punctum smithi, Glyphyalinia wheatleyi, Glyphyalinia indentata, Glyphyalinia praecox, Hawaiia minuscula, Euconulus chersinus, Euconulus dentatus, Guppya sterkii, Ventridens collisella, Ventridens gularis, Ventridens intertextus, Striatura meridionalis* and *Polygyra plicata*.

Microhabitats such as log, moss and leaf litter may provide snails with specific food requirements. Shimek (1930) concluded that snail distribution was determined chiefly by food requirements. Snails are known to aggregate as a result of localized concentrations of unicellular algae, lichens and fungi (Newell, 1967), which are usually clumped in response to local moisture conditions and/or nutrient sources. Unicellular algae flourish in some species of moss (Smith, pers. comm.), and fungi can be found around decaying logs. Fungi are believed to be the favorite food of some snails (Burch, 1956; Newell, 1967; Mason, 1970), and Wolf & Wolf (1939) provide a long list of fungi eaten by *Mesodon thyroidus*. Blinn (1963) speculated that log mold was an attractive food for some snail species. Decayed plant remains, especially leaf litter, are commonly exploited food sources (Newell, 1967; Mason, 1970), and Boycott (1934) reported finding recognizable vessels of dead leaves in the intestinal tracts of snails. Krutzsch (1952) found that the greatest number of individuals and species occurred in the forest leaf litter rather than within the A_1 horizon.

Mosses and associated snails. Although 20 snail species were found in moss, only *Vertigo gouldi* was significantly associated with this microhabitat. Fifteen moss species were collected by the liter of moss sampling method. At eight stations, two or three species of moss growing together were collected in a sample (e.g., *Bartramia pomiformis* and *Campylium chrysophyllum*) (Table 2). Only the dominant moss species sampled are given below, followed by a listing of their associated snail species.

Anomodon attenuatus: *Carychium exile, Carychium nannodes, Gastrocopta pentodon, Gastrocopta corticaria, Vertigo parvula, Vertigo gouldi, Punctum minutissimum, Glyphyalinia indentata, Hawaiia minuscula, Euconulus chersinus, Guppya sterkii, Zonitoides arboreus, Striatura meridionalis.*

Anomodon rostratus: *Gastrocopta pentodon, Vertigo gouldi, Punctum minutissimum, Punctum smithi, Glyphyalinia indentata, Hawaiia minuscula, Guppya sterkii, Striatura meridionalis.*

Aulacomnium heterostichum: *Vertigo gouldi, Hawaiia minuscula, Guppya sterkii, Striatura meridionalis.*

Bryoandersonia illecebra: *Gastrocopta pentodon, Vertigo parvula, Vertigo gouldi, Punctum minutissimum, Ventridens gularis, Striatura meridionalis, Mesodon zaletus.*

Dicranum scoparium: *Punctum minutissimum, Glyphyalinia indentata, Ventridens gularis, Striatura meridionalis.*

Eurhynchium hians: *Vertigo gouldi, Anguispira strongylodes, Glyphyalinia indentata, Striatura meridionalis.*

Fissidens taxifolius: *Striatura meridionalis.*

Hygroamblystegium tenax: *Vertigo* sp. (a single immature shell).

Hypnum fertile: *Gastrocopta pentodon, Strobilops aenea, Punctum minutissimum, Striatura meridionalis.*

Leucobryum albidum: *Gastrocopta pentodon, Guppya sterkii, Ventridens gularis.*

Mnium affine var. *ciliare*: *Guppya sterkii, Gastrodonta interna.*

Platygyrium repens: none.

Thuidium delicatulum: *Vertigo gouldi, Discus patulus, Hawaiia minuscula, Euconulus chersinus, Guppya sterkii, Striatura meridionalis.*

Rotting logs and associated snails. Those snail species significantly associated with the log microhabitat were *Gastrocopta contracta, Helicodiscus notius, Gastrodonta interna, Zonitoides arboreus, Stenotrema stenotrema, Mesodon perigraptus* and *Mesodon inflectus. Haplotrema concavum* was significantly associated with log and leaf litter microhabitats. The seven log taxa, sampled by the litter of log debris sampling method, are given below, followed by a listing of their associated snail species.

Lepidobalanus group (the white oak group): *Carychium nannodes, Gastrocopta contracta, Gastrocopta pentodon, Vertigo parvula, Columella simplex, Strobilops texasiana, Strobilops aenea, Discus patulus, Helicodiscus notius, Punctum minutissimum, Punctum smithi, Glyphyalinia cumberlandiana, Glyphyalinia wheatleyi, Glyphyalinia indentata, Euconulus chersinus, Guppya sterkii, Gastrodonta interna, Ventridens gularis, Ventridens intertextus, Ventridens elliotti, Zonitoides arboreus, Striatura meridionalis, Haplotrema concavum, Stenotrema stenotrema, Mesodon perigraptus, Mesodon inflectus.*

Erythrobalanus group (the red oak group): *Carychium exile, Cionella morseana, Gastrocopta contracta, Gastrocopta pentodon, Vertigo parvula, Strobilops aenea, Discus patulus, Helicodiscus notius, Punctum minutissimum, Glyphyalinia cumberlandiana, Glyphyalinia wheatleyi, Glyphyalinia indentata, Glyphyalinia sculptillis, Hawaiia minuscula, Euconulus dentatus, Guppya sterkii, Gastrodonta interna, Ventridens gularis, Ventridens intertextus, Zonitoides arboreus, Striatura meridionalis, Haplotrema concavum, Stenotrema stenotrema, Mesodon perigraptus, Mesodon inflectus, Triodopsis vulgata, Pomatiopsis lapidaria.*

Castanea dentata (American chestnut): *Carychium exile, Gastrocopta contracta, Gastrocopta pentodon, Anguispira strongylodes, Helicodiscus notius, Punctum minutissimum, Punctum smithi, Glyphyalinia wheatleyi, Glyphyalinia indentata, Hawaiia minuscula, Guppya sterkii, Gastrodonta interna, Ventridens gularis, Ventridens elliotti, Zonitoides arboreus, Striatura meridionalis, Haplotrema concavum, Stenotrema stenotrema, Mesodon inflectus, Pomatiopsis lapidaria*

Carya spp. (hickory spp.): *Punctum minutissimum, Glyphyalinia indentata, Guppya sterkii, Gastrodonta interna, Ventridens gularis, Zonitoides arboreus, Striatura meridionalis, Mesodon inflectus.*

Liriodendron tulipifera (tulip poplar): *Carychium exile, Punctum minutissimum, Glyphyalinia indentata, Hawaiia minuscula, Gastrodonta interna, Zonitoides arboreus, Striatura meridionalis, Haplotrema concavum.*

Aesculus octandra (sweet buckeye): *Carychium exile, Gastrocopta contracta, Anguispira strongylodes, Punctum minutissimum, Gastrodonta interna, Zonitoides arboreus, Haplotrema concavum.*

Prunus avium (bird cherry): *Gastrodonta interna, Zonitoides arboreus, Striatura meridionalis.*

Annotated list

The following species have been reported from counties in or adjacent to the study area but were not encountered in this study: *Carychium clappi* Hubricht, *Gastrocopta tappaniana* (C.B. Adams), *Vertigo oscariana* Sterki, *Strobilops labyrinthica* (Say) (Hubricht, 1973); *Succinea ovalis* Say (La Rocque, 1970); *Catinella vermeta* (Say), *Anguispira alternata* (Say), *Discus nigrimontanus* (Pilsbry), *Helicodiscus parallelus* (Say), *Punctum blandianum* (Pilsbry), *Glyphyalinia carolinensis* (Cockerell), *Glyphyalinia cryptomphala solida* H.B. Baker (Hubricht, 1973); *Glyphyalinia ocoae* Hubricht (Hubricht, 1977); *Glyphyalinia roanensis* (H.B. Baker), *Mesomphix cupreus* (Rafinesque), *Paravitrea alethia* Hubricht, *Paravitrea calciola* H.B. Baker, *Paravitrea capsella* (Gould), *Paravitrea multidentata* (Binney), *Paravitrea petrophila* (Bland) (Hubricht, 1973); *Ventridens acerra* (Lewis), *Ventridens suppressus magnidens* Pilsbry (Pilsbry, 1946); *Ventridens demissus* (Binney), *Ventridens ligera* (Say) (Hubricht, 1973); *Ventridens lawae* (W.G. Binney) (Pilsbry, 1946); *Polygyra pustuloides* (Bland), *Stenotrema barbigerum* (Redfield) (Pilsbry, 1940); *Stenotrema calvescens* Hubricht, *Stenotrema fraternum* (Say), *Stenotrema magnifumosum* (Pilsbry) (Hubricht, 1973); *Stenotrema cohuttense* (Clapp), *Stenotrema spinosum* (Lea), *Mesodon appressus* (Say), *Mesodon archeri* Pilsbry, *Mesodon downieanus* (Bland) (Pilsbry, 1940); *Mesodon clausus* (Say), *Triodopsis hopetonensis* (Shuttleworth), *Triodopsis denotata* (Férussac) (Hubricht, 1973); *Triodopsis fallax* (Say) (Pilsbry, 1940).

All species found in this study are reported in the following annotated list. However, the following information is given for those species present at four or more stations: total number of individuals and stations at which it was found; all microhabitats (leaf litter, log, moss) in which the species occurred or the 15-min search method if applicable; new county records; and determination of habitat breadth and environmental correlations and affinities based upon statistically significant environmental factors and percent presence values.

Class Gastropoda Cuvier

Subclass Pulmonata Cuvier

Order Basommatophora Keferstein

Family Carychiidae Jeffreys

Carychium exile H.C. Lea. This species was found at nine stations (343 specimens). It has a narrow habitat breadth, as it was significantly associated with six environmental factors (limestone substrata, very steep slopes, high soil moisture content, neutral soils, late stages of forest succession, and leaf litter microhabitat). It was found in the log and moss microhabitats. Bradley, McMinn and Meigs counties are new distributional records for this species.

Carychium nannodes Clapp. This species was found only at one station (27 specimens), in the log and moss microhabitats. Bradley County is a new distributional record for this species.

Order Stylommatophora Schmidt

Family Cionellidae Kobelt

Cionella morseana Doherty. This species was found only at two stations (17 specimens), in the leaf litter and log microhabitats. Meigs County is a new distributional record for this species.

Family Pupillidae Turton

Gastrocopta armifera (Say). This species was found only at one station (one specimen), in the leaf litter microhabitat. Bradley County is a new distributional record for this species.

Gastrocopta contracta (Say). This species was found at six stations (133 specimens). It has a broad habitat breadth, as it was significantly associated with but two environmental factors (very steep slopes

and log microhabitat). It was directly correlated with increasing elevation and had an affinity for neutral soils of medium moisture content, late stages of forest succession and leaf litter microhabitat. Bradley, McMinn and Meigs counties are new distributional records for this species.

Gastrocopta pentodon (Say). This species was found at 15 stations (524 specimens). It has a medium habitat breadth, as it was significantly associated with but three environmental factors (moderate and steep slopes, early stages of forest succession and leaf litter microhabitat). It had a higher affinity for dolomitic and limestone substrata than shale. It was inversely correlated with increasing elevation, slope and soil moisture. It was directly correlated with increasing soil pH. It was found in the log and moss microhabitats. Bradley, McMinn, Meigs and Polk counties are new distributional records for this species.

Gastrocopta corticaria (Say). This species was found only at two stations (three specimens). It was found only in moss (*Anomodon attenuatus*) recovered from trunks of oak trees in forests of the earliest stages of succession. Bradley and Meigs counties are new distributional records for this species.

Vertigo parvula Sterki. This species was found at eight stations (39 specimens). It has a narrow habitat breadth, as it was significantly associated with five environmental factors (limestone substrata, low elevation, steep slopes, neutral soils and leaf litter microhabitat). It was directly correlated with increasing soil moisture and pH and inversely correlated with increasing elevation. This species had an affinity for the Oak-Cedar sere and was found in log and moss microhabitats. Bradley, McMinn, Meigs and Polk counties are new distributional records for this species.

Vertigo gouldi (Binney). This species was found at nine stations (206 specimens). It has a medium habitat breadth, as it was significantly associated with four environmental factors (limestone substrata, steep and very steep slopes, neutral soils and moss microhabitat). It was directly correlated with increasing soil moisture and pH, had a greater affinity for the Oak-Cedar sere and was found in the leaf litter microhabitat. Bradley, McMinn and Meigs counties are new distributional records for this species.

Columella simplex (Gould). This species was found only at two stations (10 specimens). It was found in the leaf litter and log microhabitats. Bradley and McMinn counties are new distributional records for this species.

Family Strobilopsidae Pilsbry

Strobilops texasiana (Pilsbry & Ferriss). This species was found at five stations (38 specimens). It has a broad habitat breadth, as it was significantly associated with only one environmental factor, leaf litter microhabitat. It had an affinity for dolomitic and shale substrata, medium elevations, moderate to steep slopes, acid soils of medium to high moisture content and forests of the Oak-Pine sere, and was found in the log microhabitat. Bradley, McMinn, Meigs and Polk counties are new distributional records for this species.

Strobilops aenea Pilsbry. This species was found at seven stations (32 specimens). It was not significantly associated with any environmental factor. However, it was inversely correlated with increasing slope, soil moisture and soil pH, and had an affinity for dolomitic substrata, high elevations, forests of the Oak-Pine sere and the log microhabitat. Specimens also were found in leaf litter and moss microhabitats. McMinn and Meigs counties are new distributional records for this species.

Family Succineidae Beck

Succinea spp. Apical spires of two specimens were recovered in this study. Specific determinations were not possible, but *Succinea ovalis* Say is the probable species represented by the shells, given the Tennessee ranges of the various species of *Succinea* (Hubricht, 1973).

Catinella sp. One apical spire was recovered in this study. Specific determination was not possible, but *Catinella vermeta* (Say) is the most probable species.

Family Punctidae Morse (Endodontidae Pilsbry)

Anguispira strongylodes (Pfeiffer). This species was found at six stations (25 specimens). It has a narrow habitat breadth, as it was significantly associated with five environmental factors (limestone substrata, high elevations, very steep slopes, neutral soils and late stages of forest succession). It was directly correlated with increasing slope, soil moisture and soil pH, and had an affinity for the Oak-Cedar sere. Specimens were found by all sampling methods. Meigs and McMinn counties are new distributional records for this species.

Discus patulus (Deshayes). This species was found at eight stations (137 specimens). It was not significantly associated with any environmental factor, but it was directly correlated with increasing slope, soil moisture and soil pH, and had an affinity for late stages of forest succession. Specimens were found by all sampling methods. McMinn County is a new distributional record for this species.

Helicodiscus notius Hubricht. This species was found at eight stations (41 specimens). It has a medium habitat breadth, as it was significantly associated with three environmental factors (limestone substrata, late stages of forest succession and log microhabitat). It was directly correlated with increasing slope and inversely correlated with soil moisture and pH, and also was found in the leaf litter microhabitat. Bradley, Meigs and McMinn counties are new distributional records for this species.

Helicodiscus hadenoecus Hubricht. Formerly known only from caves of the Cumberland Plateau of Tennessee, this species was found only at one station (nine specimens). It was found only in the leaf litter and log microhabitats. Given the sharp contrast of these results with observations previously reported, this species needs further study. Meigs County is a new distributional record for this species.

Punctum minutissimum (Lea). This was one of the most abundant snail species in this study (1391 specimens from 34 stations). It has a medium habitat breadth, as it was significantly associated with three environmental factors (soils of high moisture content and neutral pH, and the leaf litter microhabitat). It had an affinity for limestone substrata and was directly correlated with increasing elevation, slope, soil moisture and pH. It was found in the log and moss microhabitats. Bradley, McMinn, Meigs and Polk counties are new distributional records for this species.

Punctum vitreum H.B. Baker. This species was found only at two stations (43 specimens). It was found only on limestone substrata, high elevations and very steep slopes, where it occurred exclusively in the leaf litter microhabitat of mesic forests. Bradley County is a new distributional record for this species.

Punctum smithi Morrison. This species was found at 10 stations (169 specimens). It has a broad habitat breadth, as it was significantly associated with only one environmental factor, the leaf litter microhabitat. It was inversely correlated with increasing elevation and directly correlated with increasing soil moisture content. This species had an affinity for dolomitic substrata and forests of the Oak-Pine sere. Specimens were found in log and moss microhabitats. Bradley, McMinn and Meigs counties are new distributional records for this species.

Family Vitrinidae Fitzinger (Zonitidae Pilsbry)

Glyphyalinia cumberlandiana Clapp. This species was found only at two stations (eight specimens). It was associated only with shale substrata, where it occurred in the log microhabitat. Bradley and Meigs counties are new distributional records for this species.

Glyphyalinia wheatleyi (Bland). This species was found at 24 stations (285 specimens). It has a medium habitat breadth, as it was significantly associated with three environmental factors (shale and limestone substrata, steep and very steep slopes, and leaf litter microhabitat). This species was directly correlated with increasing elevation, soil moisture and soil pH. It had an affinity for forests of the Oak-Cedar sere and was found in the log microhabitat. Bradley, McMinn, Meigs and Polk counties are new distributional records for this species.

Glyphyalinia indentata (Say). This species was found at 33 stations (478 specimens). It has a broad habitat breadth, as it was significantly associated with only one environmental factor, the leaf litter microhabitat. It had an affinity for shale substrata and acid to neutral soil. It was inversely correlated with increasing elevation and slope and directly correlated with increasing soil moisture content. Specimens were found by all sampling methods. McMinn and Meigs counties are new distributional records for this species.

Glyphyalinia praecox H.B. Baker. This species was found at five stations (47 specimens). It has a broad habitat breadth, as it was significantly associated with two environmental factors (medium to high levels of soil moisture content, and leaf litter microhabitat). It had an affinity for limestone substrata and late stages of forest succession, and was found by the 15-min search method. Bradley and Meigs counties are new distributional records for this species.

Glyphyalinia sculptillis (Bland). This species was found at three stations (15 specimens). It was found only in the easternmost portion of the Hiwassee River Basin close to the Blue Ridge Mountains, where it had an affinity for the Oak-Pine sere. Specimens were found in the log microhabitat and by the 15-min search method. Bradley County is a new distributional record for this species.

Mesomphix perlaevis (Pilsbry). This species was found only at two stations (30 specimens). It was found on limestone substrata, at high elevations, in forests of the Oak-Pine sere, in the leaf litter microhabitat, and by the 15-min search method. Meigs County is a new distributional record for this species.

Mesomphix latior (Pilsbry). This species was found only at two stations (29 specimens). It was found on dolomitic substrata, at medium elevations, on moderate slopes, acid soils of low moisture content, in forests of the Oak-Pine sere, in the leaf litter and log microhabitats, and by the 15-min search method. McMinn County is a new distributional record for this species.

Mesomphix capnodes (W.G. Binney). This species was found only at one station (four specimens). Meigs County is a new distributional record for this species.

Paravitrea variabilis H.B. Baker. This species was found only at two stations (34 specimens). It was found in the log and leaf litter microhabitats. Bradley County is a new distributional record for this species.

Hawaiia minuscula (Binney). This species was found at 27 stations (129 specimens). It has a broad habitat breadth, as it was significantly associated with two environmental factors (dolomitic substrata and the leaf litter microhabitat). This species was directly correlated with increasing elevation and inversely correlated with increasing soil moisture and soil pH. It was found in the log and moss microhabitats. Bradley, McMinn, Meigs and Polk counties are new distributional records for this species.

Euconulus chersinus (Say). This species was found at 15 stations (88 specimens). It has a broad habitat breadth, as it was significantly associated with only one environmental factor, the leaf litter microhabitat. It was inversely correlated with increasing elevation and soil pH, and it had an affinity for dolomitic and limestone substrata, moderate slopes, low soil moisture content, and was found in the log and moss microhabitats. Bradley, McMinn, Meigs and Polk counties are new distributional records for this species.

Euconulus dentatus (Sterki). This species was found at four stations (37 specimens). It has a narrow habitat breadth, as it was significantly associated with six environmental factors (limestone substrata, high elevations, very steep slopes, neutral soils, late stages of forest succession and the leaf litter microhabitat). This species was directly correlated with increasing soil moisture content and was found in the log microhabitat. Bradley and Meigs counties are new distributional records for this species.

Guppya sterkii (Dall). This species was found at 23 stations (340 specimens). It has a narrow habitat breadth, as it was significantly associated with six environmental factors (limestone substrata, very steep slopes, neutral soils of high moisture content, late stages of forest succession and the leaf litter microhabitat). It was directly correlated with increasing soil moisture and pH and had an affinity for forests of the Oak-Cedar sere. Specimens were found in log and moss microhabitats. Bradley, McMinn, Meigs and Polk counties are new distributional records for this species.

Gastrodonta interna (Say). This species was found at 22 stations (304 specimens). It has a broad habitat breadth, as it was significantly associated with two environmental factors (soils of medium moisture content and the log microhabitat). It had an affinity for shale substrata, acid to neutral soils and forests of the Oak-Pine sere, and was directly correlated with increasing elevation. It also was found in the leaf litter and moss microhabitats and by the 15-min search method.

Ventridens collisella (Pilsbry). This species was found at five stations (44 specimens). It has a narrow habitat breadth, as it was significantly associated with five environmental factors (high elevations, very steep slopes, neutral soils, late stages of forest succession and the leaf litter microhabitat). It had an affinity for limestone substrata and was directly correlated with increasing soil moisture and soil pH, and was found by the 15-min search method. Bradley and Meigs counties are new distributional records for this species.

Ventridens gularis (Say). This species was found at 19 stations (370 specimens). It has a broad habitat breadth, as it was significantly associated with only one environmental factor, the leaf litter microhabitat. It had an affinity for shale substrata, medium elevations, steep slopes and acid soils of medium moisture content. Specimens were found by all sampling methods. McMinn and Meigs counties are new distributional records for this species.

Ventridens lasmodon (Phillips). This species was found only at one station (18 specimens). It was found in the leaf litter microhabitat and by the 15-min search method. McMinn County is a new distributional record for this species.

Ventridens pilsbryi Hubricht. This species was found only at one station (two specimens). It was found in the leaf litter microhabitat.

Ventridens intertextus (Binney). This species was found at nine stations (67 specimens). It has a broad habitat breadth, as it was significantly associated with two environmental factors (dolomitic substrata and the leaf litter microhabitat). It was inversely correlated with increasing elevation, slope and soil moisture. It had an affinity for acid soils and early stages of forest succession. Specimens were found in the log microhabitat and by the 15-min search method. Meigs County is a new distributional record for this species.

Ventridens elliotti (Redfield). This species was found only at two stations (15 specimens). It was found in the log microhabitat and by the 15-min search method in early successional stages of the Oak-Pine sere.

Zonitoides arboreus (Say). This species was found at 25 stations (203 specimens). It has a broad habitat breadth, as it was significantly associated with only one environmental factor, the log microhabitat. It was directly correlated with increasing soil pH and had an affinity for very steep slopes, high elevations and late stages of forest succession. It was found by all sampling methods.

Striatura meridionalis (Pilsbry & Ferriss). This was the most abundant snail species in this study (1524 specimens from 37 stations). It has a broad habitat breadth, as it was significantly associated with only one environmental factor, the leaf litter microhabitat. This ubiquitous species was associated with all ranges of all environmental factors measured in this study. It also was found in the log and moss microhabitats. Bradley, McMinn, Meigs and Polk counties are new distributional records for this species.

Family Haplotrematidae H.B. Baker

Haplotrema concavum (Say). This species was found at 11 stations (50 specimens). It has a medium habitat breadth, as it was significantly associated with four environmental factors (limestone substrata, very steep slopes, late stages of forest succession, and leaf litter and log microhabitats). It was directly correlated with increasing slope and had an affinity for neutral soils of high moisture content and for the Oak-Cedar sere. Specimens also were found by the 15-min search method. McMinn County is a new county record for this species.

Family Polygyridae Pilsbry

Polygyra plicata Say. This species was found at seven stations (18 specimens). It has a medium habitat breadth, as it was significantly associated with three environmental factors (very steep slopes, oak-poplar forests and the leaf litter microhabitat). It was directly correlated with increasing slope, soil moisture content and soil pH, and had an affinity for limestone substrata and late stages of forest succession. It also was found by the 15-min search method. McMinn and Meigs counties are new distributional records for this species.

Stenotrema hirsutum (Say). This species was found at three stations (eight specimens). It was found in the leaf litter microhabitat and by the 15-min search method. Meigs County is a new distributional record for this species.

Stenotrema stenotrema (Pfeiffer). This species was found at 18 stations (45 specimens). It has a broad habitat breadth, as it was significantly associated with only one environmental factor, the log microhabitat. It was directly correlated with increasing elevation, soil moisture and soil pH, and had an affinity for steep slopes and oak-hickory-sugar maple forests. Specimens also were found in the leaf litter microhabitat and by the 15-min search method. McMinn County is a new distributional record for this species.

Mesodon thyroidus (Say). This species was found at six stations (11 specimens). It was inversely correlated with increasing slope and was found only by the 15-min search method. Meigs County is a new distributional record for this species.

Mesodon zaletus (Binney). This species was found at four stations (20 specimens). It has a medium habitat breadth, as it was significantly associated with three environmental factors (limestone substrata, very steep slopes and late stages of forest succession). It was directly correlated with increasing elevation, slope, soil moisture and soil pH. It was found in the leaf litter microhabitat, by the 15-min search method, and a single specimen was collected on a limestone outcrop where it was estivating beneath a thick, moist layer of *Bryoandersonia illecebra*, which was collected as the moss sample for that station. Bradley and Meigs counties are new distributional records for this species.

Mesodon elevatus (Say). This species was found only at one station (three specimens) and only by the 15-min search method. McMinn County is a new distributional record for this species.

Mesodon perigraptus Pilsbry. This species was found at 13 stations (34 specimens). It has a broad habitat breadth, as it was significantly associated with only one environmental factor, the log microhabitat. It was directly correlated with increasing slope and had an affinity for shale and dolomitic substrata, medium elevations and forests of the Oak-Pine sere. Specimens were collected by the 15-min search method. McMinn and Meigs counties are new distributional records for this species.

Mesodon inflectus (Say). This species was found at 33 stations (242 specimens). It has a broad habitat breadth, as it was significantly associated with two environmental factors (soils of high moisture content and the log microhabitat). It was directly correlated with increasing soil pH and soil moisture content, and was found in the leaf litter microhabitat and by the 15-min search method. Meigs County is a new distributional record for this species.

Mesodon rugeli (Shuttleworth). This species was found at three stations (26 specimens). It was found in the leaf litter and log microhabitats and by the 15-min search method.

Triodopsis vulgata Pilsbry. This species was found at five stations (19 specimens). It has a broad habitat breadth, as it was significantly associated with two environmental factors (very steep slopes and late stages of forest succession). It was directly correlated with increasing elevation and slope, and was found in the leaf litter and log microhabitats and by the 15-min search method. Meigs County is a new distributional record for this species.

Triodopsis alabamensis (Pilsbry). This species was found only at one station (eight specimens). It was found in the leaf litter microhabitat and by the 15-min search method. Meigs County is a new distributional record for this species.

Triodopsis tridentata (Say). This species was found only at one station (nine specimens). It was found by the 15-min search method. Broken shells were found in shrew runways and a short-tailed shrew was captured and released at this station.

Triodopsis caroliniensis (Lea). This species was found only at one station (three specimens). It was found by the 15-min search method. Bradley County is a new distributional record for this species.

Triodopsis albolabris (Say). This species was found only at one station (four specimens). It was found by the 15-min search method. Meigs County is a new distributional record for this species.

Subclass Prosobranchia Milne Edwards

Order Mesogastropoda Thiele

Family Pomatiopsidae Stimpson

Pomatiopsis lapidaria (Say). This species was found at four stations (51 specimens). It has a broad habitat breadth, as it was significantly associated with only one environmental factor, low elevation. It had an affinity for the Oak-Cedar sere, particularly oak-hickory-sugar maple forests, and was found in the leaf litter and log microhabitats.

DISCUSSION

In the Hiwassee River Basin of southeastern Tennessee, the most important environmental factor influencing the presence or absence of snail species (based on the total number of species which were statistically significantly associated with any given environmental factor) was microhabitat ($P < 0.05$ for 27 species). This was followed in decreasing order of importance by slope ($P < 0.05$ for 15 species), rock type ($P < 0.05$ for 13 species), stages of forest succession ($P < 0.05$ for 12 species), soil pH ($P < 0.05$ for eight species), elevation ($P < 0.05$ for seven species) and soil moisture ($P < 0.05$ for six species).

The effect of rock type on the presence or absence of snail species, the original objective of this study, was found to be third in importance compared with the other environmental factors studied. This largely is due to the fact that the geologic substrata and vegetation strongly influence the amount of calcium available to snails, as well as the amount of moisture present in the soil. Of the three rock types, limestone would provide the greatest amount of calcium to the environment by means of *"in situ"* erosion of the high calcium carbonate bedrock, and also more moisture may be available resulting from ground water conditions. Stations underlain by shale, because of rapid erosion, may equal limestone as a source for calcium, which may explain why one station underlain by shale supported more snail species than any other station investigated. Dolomites in the study area have a high silica content and are relatively poor in calcium carbonate (Maher & Milici, 1975). The two species significantly associated with regions underlain by dolomite have relatively thin shells and probably have a very high tolerance to low calcium availability. One of them (*Ventridens intertextus*) is preyed upon by a variety of predators (Ingram, 1942, 1950), and its significant association with dolomites may be the result of its extirpation from limestone regions which support dense snail faunas and, consequently, their predators.

The effect of elevation is probably only indirectly important for snails. For example, *Pomatiopsis lapidaria*, an amphibious species, cannot wander far from a water source and would more likely be found at lower elevations. The significant association of snail species for high elevations may be the indirect result of limestone substrata, which is locally responsible for higher relief.

Recently, workers have become aware of the importance of slope for some terrestrial organisms (Strahler, 1978; Dillon, 1980). Snails may be capable of detecting variations in substrate angle (Kerkut & Walker, 1975). However, slope clearly controls environmental factors which are important to snails (e.g., forest type, soil moisture, etc.) and is probably also of indirect importance to them. Slope is largely determined by the geochemical makeup of the underlying substrata, as steeper slopes typically result from harder and thus slower weathering substrata. Snails may be influenced more by the amount of calcium availability resulting from the underlying substrata than by slope alone.

In this study, slope was directly correlated with increasing soil moisture (moderate slopes: $\bar{x} = 16.6\%$; steep slopes: $\bar{x} = 22.7\%$; very steep slopes: $\bar{x} = 25.0\%$) and increasing soil pH (moderate slopes: $\bar{x} = 5.5$; steep slopes: $\bar{x} = 5.9$; very steep slopes: $\bar{x} = 6.2$). The correlation of soil pH with increasing slope was expected, since the steeper slopes are underlain by limestones. The correlation of soil moisture with increasing slope was opposite the expected result, as xeric sites usually are associated with steeper slopes (Norton & Smith, 1930). However, in the present study area, steeper slopes usually were associated with coves, which could shield sites from excessive evapotranspiration. Another factor was the capillary flow of moisture in the bedding planes of the limestone substrata underlying the steeper slopes. That such capillary flow exists is evidenced by the dense moss which covers the dripping bedrock outcrops of the Sequatchie Formation.

The only species significantly associated with soils of medium moisture content, *Gastrodonta interna*, also was significantly associated with the log microhabitat. This species is known to be a fire succession species (Archer, 1935) and obviously can colonize relatively

xeric forest habitats by its ability to survive these conditions by inhabiting the comparatively moist shelter provided by the log microhabitat. The ubiquitous species *Striatura meridionalis*, which was even present at the driest stations in this study, possesses adaptive shell structures (i.e., ribs and white epidermis) similar to those described by Evans (1972) for British snails which are capable for surviving in relatively xeric habitats. Most snail species collected in this study require relatively moist soil conditions and would not be expected in early forest successional stages or otherwise xeric habitats.

Burch (1955) contended that soil pH had little influence upon the snails and that they were more strongly influenced by physical makeup of the soil, content of available nutrients, vegetation and climate. This opinion is supported by the weak correlation of snail distribution with soil pH found in this study.

Forest successional stage, determined in part by the presence or absence of indicator tree species, appears partially to influence snails by providing food, calcium and shelter. Nearly pure pine forests are known to be very poor habitats for snails (Pilsbry, 1892; Jacot, 1935; Burch, 1956). The adverse effect of pines upon snails is due in part to forest structure and the resulting lower ambient moisture, and may in part result from the comparatively low concentration of calcium in freshly fallen pine leaf litter (Lutz & Chandler, 1946). The effect of pure cedar upon snails is unknown. However, cedar (*Juniperus virginiana*) foliage contains nearly twice the amount of calcium found in pine foliage (Van Camp, 1948), and it possibly could provide a more conducive environment than pine for snails. American chestnut (*Castanea dentata*) is the only other species of tree known to have a negative influence upon snails (Winslow, 1921), and it is possible that the removal of the American chestnut by the Chestnut Blight had a beneficial effect upon snails. Dogwood (*Cornus florida*), a disturbance indicator, is known to have a very high calcium content (Van Camp, 1948), a further indication that forest disturbance may have a beneficial effect upon snails. Oak forests are known to have a favorable influence upon the distribution and abundance of snails (Winslow, 1921; Archer, 1939a; Burch, 1956-57).

In this study, the presence of American beech (*Fagus grandifolia*) appeared to affect adversely the abundance of snails (Fig. 2). This inverse relationship may be the result of the amount and organic form of calcium present, as well as the length of time required for the breakdown of leaves. The leaf litter of *Fagus grandifolia* had the lowest calcium content of hardwood species listed by Lutz & Chandler (1946), and only species of *Pinus* are known to contain less calcium than *Fagus*. In nature, leaves of ash, maple and elm contain calcium citrate, while leaves of oak and beech contain the less soluble calcium oxalate (Wäreborn, 1979). Wäreborn (1979) showed that snail reproduction was increased by the artificial additions of calcium citrate and calcium oxalate, the former being significantly better than the latter. Edwards & Heath (1975) found that oak leaves broke down much more rapidly and were much more palatable to a variety of soil animals than were beech leaves. Beech leaf litter has a very low leaf content of calcium, which occurs as the less favorable form of calcium oxalate, and palatability is decreased as a result of comparatively slow rate of leaf decomposition.

As *Fagus grandifolia* increased in importance in the stands sampled, snail abundance decreased. In addition, the numbers of individuals of *Glyphyalinia wheatleyi* were inversely correlated with increasing importance values of *Fagus grandifolia* in stands sampled. This effect is even more dramatic where the underlying geologic substrata is relatively low in calcium (i.e., shales and dolomites) (Fig. 2). Wäreborn (1979) observed that snails may depend on the presence of tree species rich in calcium citrate where the underlying geologic substrata consisted of non-calcareous metamorphic rocks. Conversely, snails may be better able to adapt to forests which are dominated by calcium-poor tree species (e.g., *Fagus grandifolia*) where calcium is supplemented by soils derived from calcareous limestone substrata.

Of the three types of microhabitats studied, leaf litter was the most commonly inhabited

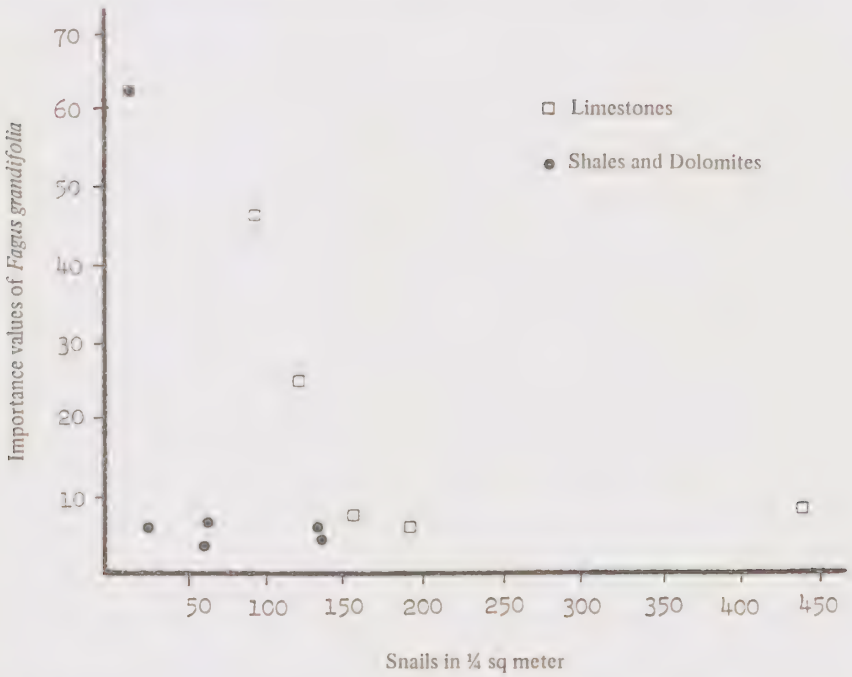

FIG. 2. Snail densities on shale and dolomite substrata as compared with those of limestone at stations where *Fagus grandifolia* was present.

and apparently was important as a food source. The leaves of many hardwoods contain appreciable amounts of calcium (Lutz & Chandler, 1946). Many snails are able to obtain calcium from leaf litter (Wäreborn, 1979) and may be able to compensate in this manner where soils are poor in calcium. Generally smaller species inhabited the log microhabitat. Snails having affinities for the log microhabitat were found under nearly all log taxa studied and probably are adapted to specific moisture regimes and/or food requirements rather than to differences in chemical properties of the decaying log taxa.

Although mosses have been recommended as worthy of inspection for snails (Sterki, 1887), no significant associations have been reported by previous workers. *Anomodon* spp., *Bryoandersonia illecebra* and *Thuidium delicatulum* share the ecological classification of "mats" according to Smith (pers. comm.), defined by Gimingham & Robertson (1950) as "systems forming a relatively thin, generally dense and interwoven mat, closely adpressed to substratum." Mosses of the "tall turf" ecotype (Gimingham & Robertson, 1950) were *Aulacomnium heterostichum* and *Dicranum scoparium*, as determined by Smith (pers. comm.), and were inhabited by snails to a much lesser extent. *Leucobryum albidum*, a "cushion" ecotype of Gimingham & Robertson (1950), was inhabited even less than "mat" or "tall turf" ecotypes.

Anomodon rostratus and *Bryoandersonia illecebra* are high in calcium content (Shacklette, 1965). In addition, *Anomodon attenuatus*, *Anomodon rostratus* and *Eurhynchium hians* were reported to be relatively neutral in pH (Montgomery, 1931). *Thuidium delicatulum* and *Bryoandersonia illecebra* showed similar results (Ikenberry, 1936). *Dicranum scoparium* and *Platygyrium repens*, however, have been reported to be acidic in pH (Ikenberry, 1936). Snails are not known to ingest moss. High calcium content and neutral pH of some moss species could serve as an environmental buffer for snails in perhaps an otherwise acidic environment.

Intrageneric relations

The intrageneric associations of common snail species were statistically tested (Table 7), using the chi-square test and test of association (V) (Krebs, 1972) to determine the extent and direction of association of congeneric species. The results of all four sampling methods were combined for each station in order to determine presence or absence of a given species. Species tested were present at a minimum of four sampling stations. In addition, affinities for environmental factors, based on highest relative frequency (i.e., percent presence), were compared for congeneric snail species to determine how these species partitioned their environment (Table 8).

The chi-square test and test of association (V) statistically measure the degree of association of two species based on presence/absence data. Negatively associated species (e.g., V = -0.43) generally do not share station occurrence, while positively associated species (e.g., V = 0.31) generally do. Because physical factors and forest types differ from station to station, one would expect that congeneric species which were negatively associated also would differ more or less in terms of their respective affinities. Only the microhabitat (leaf litter, moss and log) was equally different at each station, yet relatively identical in structure from station to station (i.e., all stations were sampled for each microhabitat). Differences in leaf, moss and log species composition may influence the presence or absence of snail species. However, statistical tests indicated that while certain snail species were significantly associated with logs as a microhabitat, no species was significantly associated with any given log taxon.

Intrageneric relationships can be grouped into four categories: (1) those congeneric species which share microhabitat affinity and have positive (V) association values; (2) those which share microhabitat affinity and have negative (V) association values; (3) those which differ in microhabitat affinity and have positive (V) association values; and (4) those which differ in microhabitat affinity and have negative (V) association values.

Closely related species may coexist in the same habitat if occupying different niches. Proof of this axiom exists for certain congeneric snail species studied. One might expect congeneric species to be inhabiting different microhabitats if they are positively associated for station presence. This can be clearly observed by comparing the following congeneric species which are positively associated and which have different microhabitats (Table 7): *Vertigo parvula* (leaf litter)/*Vertigo gouldi* (moss) -V = 0.31; *Strobilops aenea* (leaf litter)/*Strobilops texasiana* (log) -V = 0.21; *Mesodon zaletus* (leaf litter)/*Mesodon inflectus* (log) -V = 0.12. Furthermore, *Vertigo parvula* and *Vertigo gouldi* differ in only two physical factors.

Conversely, congeneric species which do not differ in microhabitat may in fact differ in their affinities for physical factors or forest type and may be negatively associated for station presence. This can be observed by comparing physical factors and forest type for the following congeneric species which are negatively associated and which have similar microhabitats (Table 7): *Glyphyalinia indentata/Glyphyalinia praecox* (-V = -0.34, five affinities differ); *Euconulus chersinus/Euconulus dentatus* (-V = -0.29, six affinities differ); *Ventridens collisella/Ventridens gularis* (-V = -0.43, six affinities differ); *Ventridens collisella/Ventridens intertextus* (-V = 0.04, six affinities differ); *Ventridens gularis/Ventridens intertextus* (-V = -0.11, five affinities differ). Of these, *Glyphyalinia indentata/Glyphyalinia praecox* and *Ventridens collisella/Ventridens gularis* were significantly negatively associated. That the tested congeneric species of *Ventridens* exhibited a high amount of negative association is interesting in the light of the following sagacious advice: "If you want an interesting ecological problem to work on, find out what keeps the species of *Ventridens* apart" (Leslie Hubricht, pers. comm.).

Congeneric species which are different in microhabitat type and yet are still negatively

TABLE 7. Comparisons of congeneric species using Chi-square test of independence and test of association.

	Gastrocopta pentodon	*Vertigo gouldi*	*Strobilops texasiana*	*Punctum smithi*	*Glyphyalinia indentata*	*Glyphyalinia praecox*	*Euconulus dentatus*	*Ventridens gularis*	*Ventridens intertextus*	*Mesodon zaletus*	*Mesodon perigraptus*	*Mesodon inflectus*
Gastrocopta contracta	0.15[1] -0.06[2]											
Vertigo parvula		3.66 0.31										
Strobilops aenea			1.67 0.21									
Punctum minutissimum				1.21 0.18								
Glyphyalinia wheatleyi					0.00 0.01	0.58 0.13						
Glyphyalinia indentata						4.37* -0.34						
Euconulus chersinus							3.06 -0.29					
Ventridens collisella								6.80** -0.43	0.06 -0.04			
Ventridens gularis									0.44 -0.11			
Mesodon thyroidus										0.87 -0.15	1.07 -0.17	0.25 -0.08
Mesodon zaletus											0.20 -0.07	0.54 0.12
Mesodon perigraptus												0.20 0.07

[1] X^2 value
[2] V value

*Significant P⟨.05
**Significant P⟨.01

TABLE 8. Comparisons of congeneric species by highest relative frequencies for environmental factors.

Species	Rock type			Elevation			Slope		
	Shale	Dolo-mite	Lime-stone	Low	Medium	High	Moderate	Steep	Very steep
Gastrocopta contracta			X			X			X
Gastrocopta pentodon			X	X			X		
Vertigo parvula			X	X				X	
Vertigo gouldi			X			X		X	
Strobilops aenea		X				X	X		
Strobilops texasiana	X				X		X		
Punctum minutissimum			X			X			X
Punctum smithi		X		X				X	
Glyphyalinia wheatleyi	X					X		X	
Glyphyalinia indentata	X			X			X		
Glyphyalinia praecox			X	X				X	
Euconulus chersinus		X		X			X		
Euconulus dentatus			X			X			X
Ventridens collisella			X			X			X
Ventridens gularis	X				X			X	
Ventridens intertextus		X		X			X		
Mesodon thyroidus		X			X		X		
Mesodon zaletus			X			X			X
Mesodon perigraptus	X				X				X
Mesodon inflectus	X					X		X	

X = highest relative frequency.

associated for station presence (*Gastrocopta contracta/Gastrocopta pentodon* and *Mesodon zaletus/Mesodon perigraptus*) are very different in forest successional stages.

Congeneric species which are similar in microhabitat type and positively associated (*Punctum minutissimum/Punctum smithi*; *Glyphyalinia wheatleyi/Glyphyalinia indentata*; *Glyphyalinia wheatleyi/Glyphyalinia praecox*; and *Mesodon perigraptus/Mesodon inflectus*) may differ in methods of utilizing environmental resources which were not evaluated in this study (e.g., seasonally different reproductive periods, different habitational levels in the leaf litter microhabitat, etc.). Curiously enough, the systematics of *Punctum minutissimum* and *Punctum smithi* are based on shell characters alone and there is no concrete evidence that the

TABLE 8 (Cont.)

Soil moisture			Soil pH			Forest succession			Microhabitat		
Low	Medium	High	Very acid	Acid	Neutral	Early	Late	Non-specific	Leaf litter	Moss	Logs
	X				X		X				X
X					X	X			X		
		X			X	X			X		
		X			X	X				X	
X			X			X			X		
	X			X		X					X
		X			X			X	X		
		X	X		X	X			X		
		X			X			X	X		
		X		X			X		X		
	X		X		X		X		X		
X			X					X	X		
		X			X		X		X		
		X			X		X		X		
	X			X				X	X		
X				X		X			X		
-[1]	-[1]	-[1]	-[1]	-[1]	-[1]	X			-[2]	-[2]	-[2]
		X			X		X		X		
-[1]	-[1]	-[1]	-[1]	-[1]	-[1]	X					X
		X			X			X			X

[1] Species absent from tested ¼ sq m samples.
[2] Species found only by timed search method.

two are good species; in fact, shell differences due to shell thickness and umbilicus diameter may be based on calcium availability alone (Gould, 1971).

These congeneric species show different patterns of adaptive coexistence. Some can share the same general habitat by differing in affinities for microhabitats. Others, which show no obvious difference in microhabitats, differ dramatically in affinities for physical environmental factors and/or forest type and appear to avoid intrageneric interaction (e.g., competition) by avoiding co-occurrence. These findings do not support Boycott's (1934) conclusion that the competition does not exist among snails for food and shelter.

The analysis of snail ecology can be very difficult for several reasons. Rates of migration may be quite different due to size differences among species. The relative ability to adapt physiologically to environmental change also may influence migration rates. Evans (1972) noted that the rate of colonization was a function of species abundance, type of terrain and rate of dispersal. He also noted that snail populations are constantly changing their distribution, extending and contracting in an "amoeboid fashion".

Further study should include extensive sampling of mosses for their associated snail species, comparison of snail populations in stands of *Fagus grandifolia* in calcareous and non-calcareous regions, electrophoretic and genetic studies of the genus *Punctum*, and further investigation of the effect of slope on the ecology and physiology of snails.

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MORPHOLOGY AND TAXONOMY OF TWO SPECIES OF THE GENUS *TRANSENNELLA* (BIVALVIA: VENERIDAE) FROM WESTERN NORTH AMERICA AND A DESCRIPTION OF *T. CONFUSA* SP. NOV.

Susan Gray[1]

ABSTRACT

The genus *Transennella* Dall 1883 is represented on the west coast of the United States by two morphological entities whose systematic status has been in question. Examinations of shell form and soft-part anatomy, as well as ecological observations, support the recognition of the two entities as separate species. The two species may be separated on the basis of shell outline, pigmentation, sculpture, shape of the hinge plate and strength of the hinge teeth, fused or split siphons and the length of the intestine. Consultation of type specimens and taxonomic literature resulted in the description of *T. confusa* sp. nov. and the designation of a neotype for *T. tantilla* (Gould 1852). The species occur sympatrically along the coasts of Oregon and California, U.S.A.

INTRODUCTION

The genus *Transennella* was established by Dall in 1883. The type species (by monotypy) is *T. conradina* Dall 1883, which occurs in the Caribbean and in Miocene deposits in Florida. The key characteristics of the genus are a hinge with three cardinal teeth in each valve, of which the middle cardinal tooth is bifid; an elongated anterior lateral tooth in the left valve; an angular pallial sinus; and tangentially grooved inner ventral margin of the shell.

All known described members of the genus are restricted in distribution to the New World. There are two fossil species (*Transennella californica* Arnold; *T. joaquinensis* Anderson & Martin) and 12 Recent species. Of the Recent species, four occur in the Caribbean (*T. conradina* Dall; *T. cubaniana* d'Orbigny; *T. culebrana* (Dall & Simpson); *T. stimpsoni* Dall), seven in the eastern Pacific off the coasts of Central and South America (*T. caryonautes* Berry; *T. galapagana* Hertlein & Strong; *T. humilis* (Carpenter); *T. modesta* (Sowerby); *T. omissa* (Pilsbry & Lowe); *T. pannosa* (Sowerby); *T. puella* (Carpenter)), and one off the coast of central California. The central California species was described as *Venus tantillus* by Gould in 1852. Subsequent revisions (see Carpenter, 1864; Dall, 1902) placed this bivalve in the genus *Transennella*.

The available literature on the genus *Transennella* on the west coast of the United States consists of a few locality records (Dall, 1902; Keen & Coan, 1974), a series of experiments on sediment type and feeding relationships (Maurer, 1967a,b,c; 1968) and studies on its resistance to burial (Gallucci & Kawaratani, 1975). A study on the seasonal respiration of *T. tantilla* by Pamatmat (1969), plus the previously mentioned studies, constitutes the only ecological research on the animal. Hansen (1953) described the occurrence of protandrous hermaphroditism in a population of *T. tantilla* in False Bay, Washington. Aspects of the morphology of *T. tantilla* were compared with *Gemma gemma* (Totten 1834) in a paper by Narchi (1971).

In the early 1970's, two distinct morphological varieties of *Transennella tantilla* were noted in Bodega Bay, Sonoma County, California, and Tomales Bay, Marin County, California (Steve Obrebski, pers. comm.). The varieties coexisted in these locations and were

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separable on the basis of shell pigmentation and shell shape. Speculation on whether or not the two varieties were separate species or one polymorphic species led to several student projects on ecological relationships (Kaufman & Zeitlan, 1971; Brian Stagl, pers. comm.) and isozyme analysis (Bill Rotz, pers. comm.). None of the published accounts on *T. tantilla* mention any variation in shell morphology, although Dall (1902) did note differences in the degree of pigmentation in *T. tantilla* in the northern end of its range.

Comparisons of both shell and soft-part morphology plus ecological observations support the separation of the two varieties into distinct species. This paper describes a new species of *Transennella* from the northeastern Pacific and compares various aspects of its morphology with that of *T. tantilla*.

MATERIALS AND METHODS

Specimens of *Transennella* were collected monthly during 1977 from Lawson's Flat, Tomales Bay, Marin County, California, U.S.A. The majority of the specimens were preserved in 75% ethanol or 10% buffered formalin for dissection and to serve as reference material. Specimens collected in July and August of 1977 were preserved in Bouin's solution for histological examination. Living animals were used to study ciliary currents and siphon function. Shell morphology was examined with the aid of an ETEC Autoscan electron microscope located in the Department of Biological Sciences, San Francisco State University. Occasional collections also were made at Bodega Bay, Sonoma County, California, and Princeton Harbor, San Mateo County, California.

Specimens of all described species of *Transennella*, as well as those covering the geographic range of the northeastern Pacific *Transennella*, were examined in order to provide the proper name(s) for each species. Shell material was examined from the collections of the California Academy of Sciences, San Francisco (CAS), Los Angeles County Museum of Natural History (LACM), National Museum of Natural History, Smithsonian Institution (USNM), and the Museum of Comparative Zoology, Harvard (MCZ).

TAXONOMY

The following are descriptions of the northeastern Pacific species of *Transennella*.

Transennella tantilla (Gould 1852)
(Fig. 8, Neotype)

Venus tantillus Gould, 1852. *Bost. J. nat. Hist.*, 6: 408. (Santa Barbara).
Venus rhysomia Gabb, 1861. *Proc. Acad. nat. Sci. Phila.*, 13: 369.
Psephis tantillus in Carpenter, 1864. *Rep. Br. Assoc. Adv. Sci. for 1863*, p. 632.
Transennella tantilla in Dall, 1902. *Proc. U.S. natl. Mus.*, 26: 384.

Description. "Shell quite small, rather solid, ovate trigonal, inequilateral; beaks acute; surface smooth or faintly waved with distinct concentric furrows; the dorsal margins are nearly straight and meet at the apex in a right angle, but the posterior side is a fourth longer than the anterior; the anterior basal margin is well rounded, while the posterior is acute, basal margin gently curved. Color white, but the posterior third is stained a deep slatey blue outside and in, the line of demarcation is quite abrupt and well defined; there is also a pencil of the same color inside, running from the beak to the anterior cicatrix, the rest of the interior is cream colored. Length one-fourth of an inch, height one-fifth of an inch" (Gould, 1852: 408, pl. 15, fig. 10).

The species may be described additionally as:

Shell (exterior): Valves equal, beak rounded, situated approximately 40% of total length from anterior end; lunule faint, no ecsutcheon; ligament opisthodetic and parivincular; concentric sculpture; mean length 5.12 mm, mean height 4.23 mm (n=88).

Shell (interior): Adductor scars subequal; anterior slightly larger than posterior; pallial sinus rounded, extending anteriorly beneath the posterior cardinal tooth; ventral margin

smooth, with few oblique grooves; hinge plate wide, extending straight across dorsal end of shell; three cardinal teeth in each valve, middle cardinal tooth bifid; anterior lateral tooth in left valve, corresponding socket in right valve.

Soft parts: Mantle thin, margin consisting of four folds; two siphons present, split along one-half their length; small tentacles present on distal end of both incurrent and excurrent siphons; foot large, byssal gland functional in adult; stomach simplified, with reduced dorsal pouch; style sac and intestine combined; intestine forms small loop under stomach.

Dimensions: Neotype USNM 749090 (P.P. Carpenter No. 367): shell length 3.8 mm, shell height 3.0 mm.

Type locality. Santa Barbara, California. Collector: E. Jewett. (No date of collection given.)

Range. Sitka, Alaska, to Lower California, Todos Santos Bay (Dall, 1902). Specimens of *Transennella tantilla* examined for this study ranged from Receta Island, Alexander Arch., Alaska (LACM, uncataloged), to Cabo San Lucus, Baja California (CAS 27587).

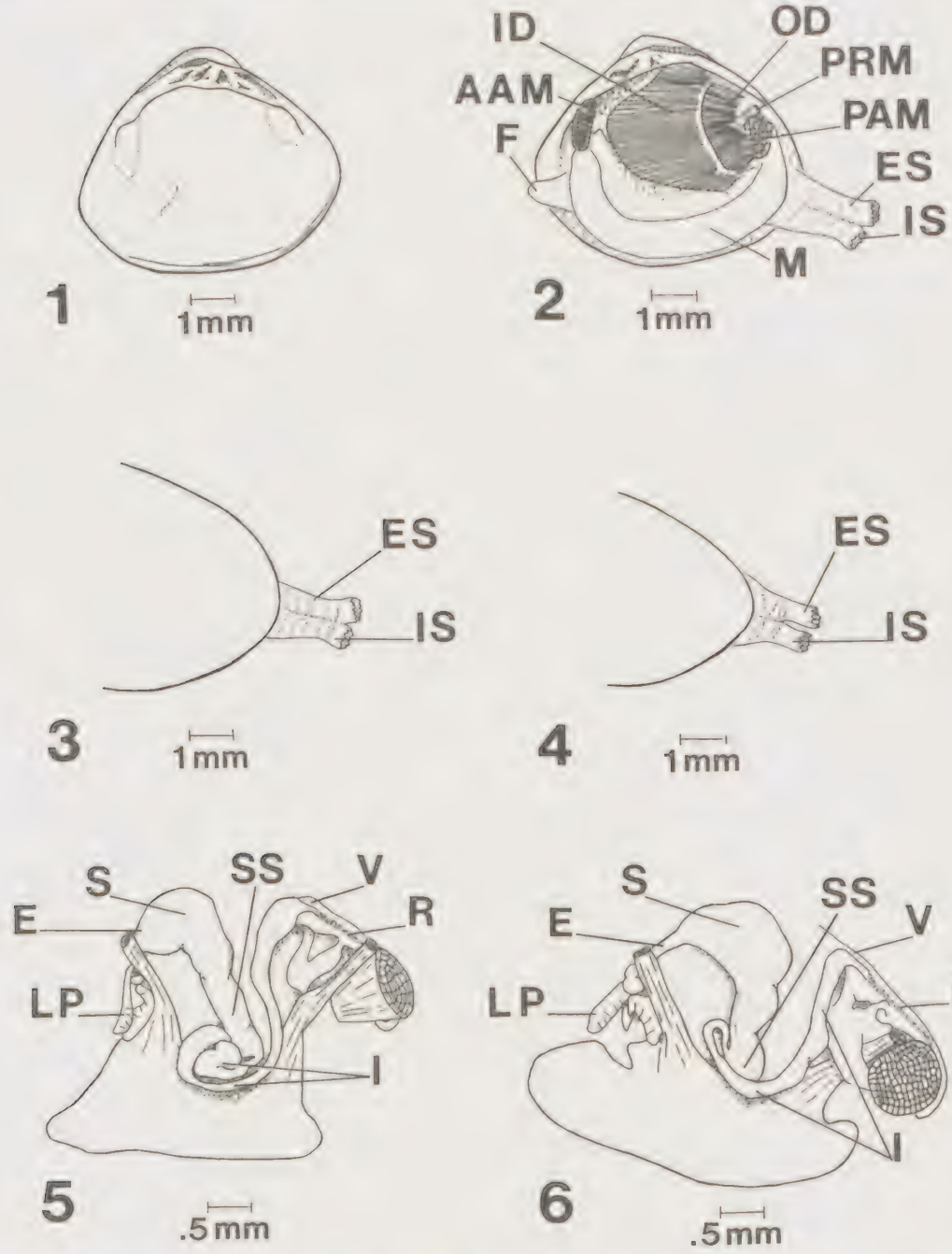
Discussion. Examination of the specimen declared by Johnson (1964) to be the holotype of *Transennella tantilla* (MCZ 169391) led to the discovery that the specimen is in fact not *T. tantilla* but a juvenile specimen of *Tivela stultorum* (Mawe 1823). The accompanying data with the "holotype" includes labels from the New York State Museum, cat. no. 358, a label from the A.A. Gould Type Collection No. A4612, and a note in what appears to be Gould's handwriting giving the locality and a specimen number of 14. According to Carpenter (1864), this is Gould's manuscript number. However, the specimen does not in any manner match the type description or figure given by Gould and is probably a product of subsequent mixing of specimens. The Museum of Comparative Zoology did not contain any additional specimens of *Transennella tantilla* that could be ascribed to the missing holotype (Kenneth Boss, pers. comm.). Subsequent searches did not reveal the specimen at the National Museum of Natural History, Smithsonian Institution (Joseph Rosewater, pers. comm.), the American Museum of Natural History (William Emerson, pers. comm.) or the Academy of Natural Sciences of Philadelphia (Melanie Miller, pers. comm.), and it appears that the specimen is lost.

I also have attempted to recover the specimen described by Gabb (1861) as *Venus rhysomia*, which he later synonymized with *Transennella tantilla*. The specimen was not found at the Academy of Natural Sciences of Philadelphia (Elizabeth Scott, pers. comm.) nor at the American Museum of Natural History (William Emerson, pers. comm.). Some of Gabb's specimens have been deposited at the Museum of Paleontology, University of California at Berkeley, but the specimen was not located in that collection (Joseph Peck, pers. comm.). To stabilize the name *Transennella tantilla*, I have selected a specimen from the P.P. Carpenter collection (USNM 749090) that was collected in the same place and by the same collector as Gould's holotype and hereby designate it the **neotype** of *Transennella tantilla* (Fig. 8).

Transennella confusa Gray, sp. nov.
(Figs. 1, 2, 7, Holotype; Fig. 5, Paratype)

Description. **Shell** (exterior): Ovate-trigonal; valves equal; inequilateral; beak prominent, situated approximately 40% of total length from anterior end; dorsal margin concave just anterior to beak; lunule faint, no ecsutcheon; ligament opisthodetic and parivincular; sculpture weak, consisting of closely spaced fine concentric lines; color white, with an occasional brown patch just anterior to beak; mean length 5.32 mm, mean height 4.32 mm (n= 88).

Shell (interior): Adductor scars subequal; anterior slightly larger than posterior; pallial sinus rounded, extending anteriorly beneath the posterior cardinal tooth; ventral margin smooth with few oblique grooves; hinge plate narrow, curving along dorsal margin; three



FIGS. 1, 2. Holotype, *Transennella confusa*, CAS 015608. FIG. 1. Internal view, left valve. FIG. 2. Left side, soft-part morphology. FIGS. 3, 4. Siphons. FIG. 3. *T. confusa*, relaxed, preserved specimen. FIG. 4. *T. tantilla*, relaxed, preserved specimen. FIGS. 5, 6. Digestive system. FIG. 5. Paratype, *T. confusa*, CAS 015610. FIG. 6. *T. tantilla*.

Abbreviations: AAM, anterior adductor muscle; E, esophagus; ES, excurrent siphon; F, foot; I, intestine; ID, inner demibranch; IS, incurrent siphon; LP, labial palps; M, mantle; OD, outer demibranch; PAM, posterior adductor muscle; PRM, posterior retractor muscle; R, rectum, S, stomach; SS, style sac; V, ventricle.

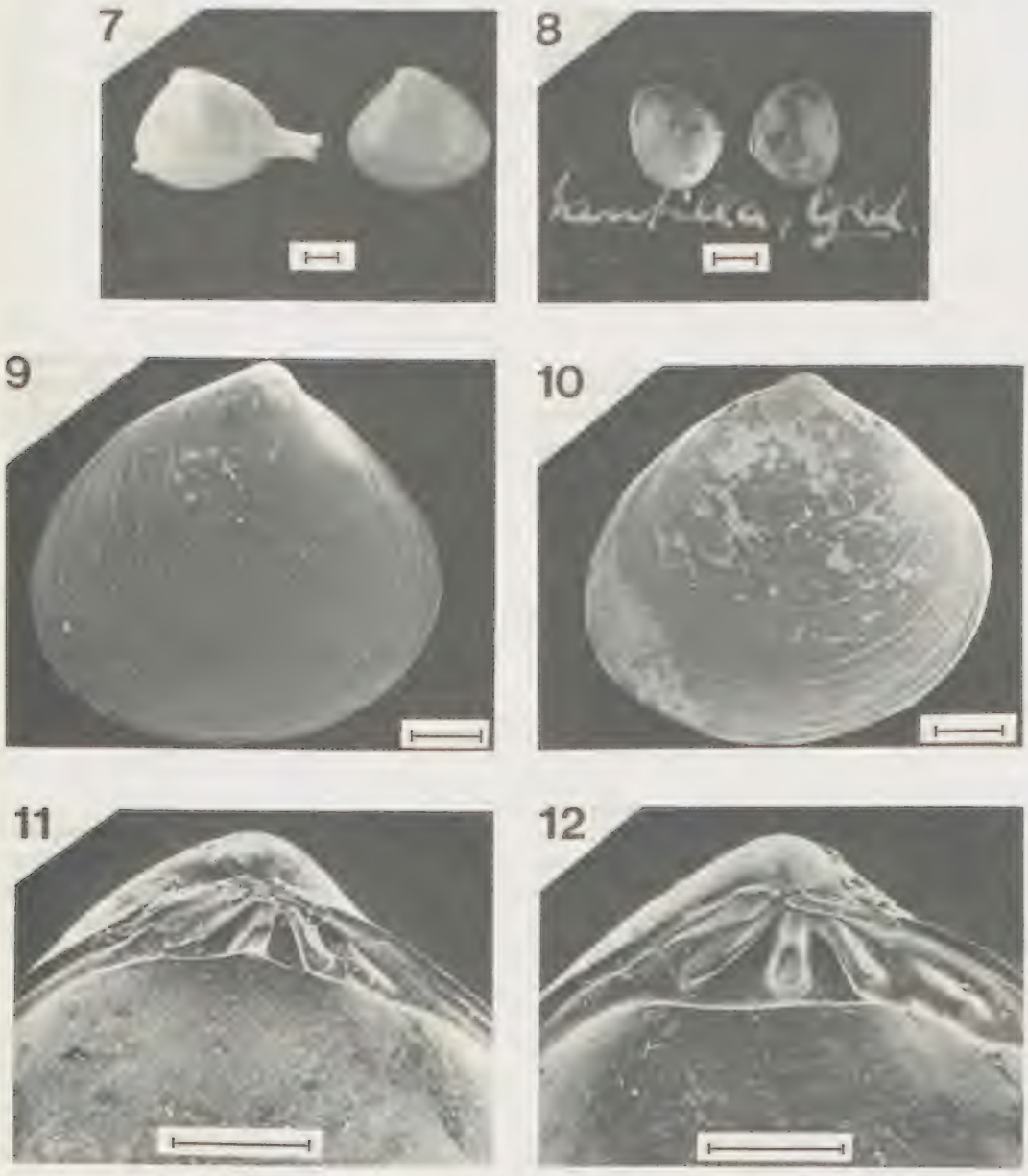


FIG. 7. Holotype, *Transennella confusa*, CAS 015608. Scale = 1 mm. FIG. 8. Neotype, *T. tantilla*, USNM 749090. Scale = 1 mm. FIGS. 9-12. Scanning electron micrographs, shells. FIG. 9. *T. confusa*, external view, right valve, sculpture. FIG. 10. *T. tantilla*, external view, right valve, sculpture. Scale for Figs. 9, 10 = 1 mm. FIG. 11. *T. confusa*, internal view, left valve, hinge. FIG. 12. *T. tantilla*, internal view, left valve, hinge. Scale for Figs. 11, 12 = 0.5 mm.

cardinal teeth in each valve; middle cardinal tooth bifid; anterior lateral tooth in left valve, corresponding socket in right valve.

Soft parts: Mantle thin, margin consisting of four folds; two siphons present, fused along four-fifths of siphon length; small tentacles present on the distal end of both incurrent and

excurrent siphons; foot large, byssal gland functional in adult; stomach simplified, with reduced dorsal pouch; style sac and intestine combined; intestine coiled tightly under stomach.

Dimensions: Holotype CAS 015608, shell length 5.8 mm, shell height 5.2 mm. Paratypes: CAS 015609, shell length 8.3 mm, shell height 6.4 mm; CAS 015610 (Fig. 5), shell length 6.9 mm, shell height 6.2 mm; USNM 802337, 22 specimens; ANSP A8735, 22 specimens; MCZ 288860, 22 specimens; LACM 1950, 22 specimens.

Type locality. Lawson's Flat, Tomales Bay, Marin County, California. 38°13'N, 122°57'W. Intertidal. Collected 10 August 1979 by S. Gray.

Etymology. The name selected, *confusa*, an adjective (Latin: *fusa*, to fuse or be fused; *con*, with) describes the diagnostic character of the species, viz., the fused siphons.

Range. Coos Bay, Oregon (CAS 019054), to Carmel Bay, California (CAS 24830).

Diagnosis. The small adult size, weak sculpture and lack of pigmentation readily separate *Transennella confusa* from the majority of other species of the genus. Of the 14 known species of *Transennella*, *T. confusa* most closely resembles *T. californica* Arnold, a fossil species from California, and *T. tantilla* Gould (details of the comparative morphology of *T. confusa* and *T. tantilla* are presented in the next section).

Transennella confusa can be separated from *T. californica* by several shell characteristics. The overall outline of *T. confusa* is more ovate than that of *T. californica*. Both species have a prominent beak, but the beak of *T. californica* is turned anteriorly. The sculpture on *T. confusa* is weak, the lunule faintly defined, while *T. californica* has well-defined concentric sculpture and a deeply incised lunule. Interiorly, *T. confusa* has a narrow hinge plate and *T. californica* has a broad hinge plate. Both species have three cardinal teeth and an anterior lateral tooth socket in the right valve, but the middle cardinal tooth is straight in *T. confusa*, and it is bowed in *T. californica*.

Another fossil species occurring in California is *Transennella joaquinensis* Anderson & Martin. This species can be separated from *T. confusa* by its very strong concentric sculpture, concave anterior side, well-defined lunule, and very narrow and straight hinge plate.

Other Recent species that have superficial resemblance to *Transennella confusa* are *T. conradina* Dall and *T. cubiana* d'Orbigny, both of which occur in the Caribbean. *T. conradina* has distinct concentric sculpture, is rostrate, and has a deep pallial sinus. Some specimens also have a chevron pigmentation. *T. cubiana* has a thick shell that has distinct concentric sculpture and some radial sculpture at the anterior and posterior ends of the shell. These two species are separated easily from *T. confusa*.

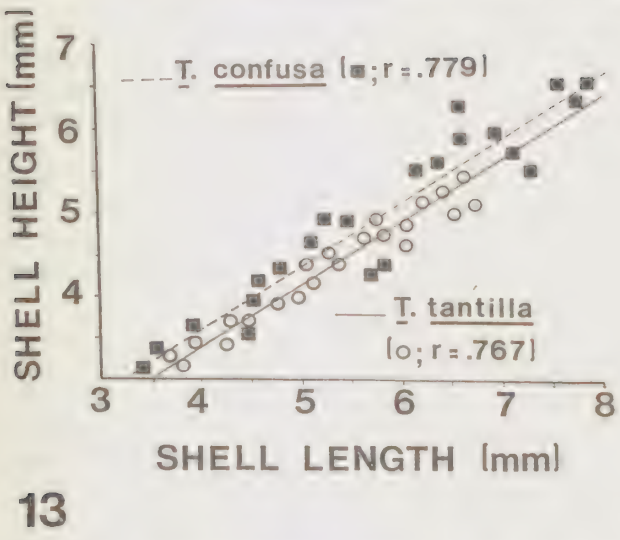
COMPARATIVE MORPHOLOGY

Members of the genus *Transennella* from the central California coast are consistent in shell form and soft-part morphology with other members of the family Veneridae. They are unusual in that byssal thread production is maintained by adults (Narchi, 1970), but otherwise are typical in all aspects.

Both shell and soft-part morphology were studied in detail. The reproductive, nervous and circulatory systems are essentially the same for both species and will not be discussed further (for more detail on these systems in *Transennella* and other venerids, see Ansell, 1961; Sellmer, 1967; Narchi, 1971; Gray, 1978). Areas that differed between the species include shell form, the siphons and the digestive system.

Shell

External. The shell shape of *Transennella confusa* and *T. tantilla* are very similar in outline, and there is no statistically significant difference in the regression values of height on length between the species (Fig. 13). However, *T. confusa* has a concavity just anterior to the beak. This gives a more prominent appearance to the beak. The sculpture pattern of *T. confusa* consists of faint, closely spaced concentric lines (Fig. 9), while that of *T. tantilla*



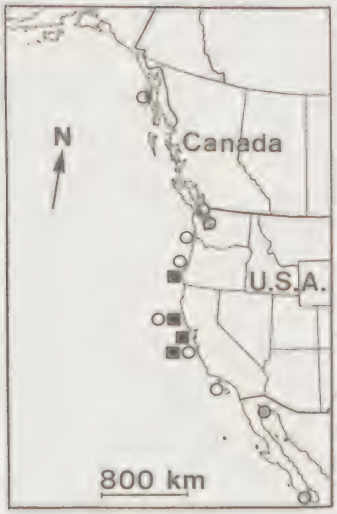


FIG. 13. Graph of regression analysis of shell length on shell height. *Transennella confusa* (■; dashed line) r = .779. *T. tantilla* (○; solid line) r = .767. FIG. 14. Distribution of *T. confusa* (■) and *T. tantilla* (○) along the coast of western North America.

consists of readily discernible, distinct concentric lines that are evenly spaced (Fig. 10).

Internal. The location and shape of the muscle scars are the same for both species. Both possess a rounded pallial sinus, extending anteriorly beneath the posterior cardinal tooth. The oblique grooves on the ventral margin of the shell that are characteristic for the genus *Transennella* are faint and not easily seen.

Differences in the shape of the hinge plate and strength of the hinge teeth are evident between the species. The hinge plate of *Transennella confusa* is narrow and curving, following the dorsal margin of the shell (Fig. 11). The teeth are thin and fragile in aspect, with the anterior lateral tooth appearing as a lamellar structure. The hinge plate of *T. tantilla* is wide and runs straight across the dorsal end of the shell (Fig. 12). The teeth are robust and the anterior lateral tooth is well defined. These differences occur consistently in all specimens examined, but are best observed on specimens greater than 2.5 mm in length.

Siphons

The differing morphologies of the siphons of the two species provide a series of diagnostic characteristics separating the two species. The siphons of *Transennella confusa* are fused to just below the tips, with only a slight area of separation (Fig. 3). Both the incurrent and excurrent siphons bear tentacles on the distal end, with the number on the excurrent siphon varying from 10-14 and the number on the incurrent siphon varying from 11-16. The tentacles on the incurrent siphon are short and broad. When the animal is actively pumping water, the incurrent siphon is completely expanded in diameter with the tentacles held out straight. The tentacles come into contact only with those particles that are very large or that enter from the sides.

The siphon body and tentacles are translucent, with many transverse white patches. There is a brown pigment at the base of each tentacle, and lining the small area of the siphon split. When the siphons are fully extended, the angle of divergence of the siphon tips is approximately 20°. The siphons are sensitive to touch, light intensity and water turbidity.

The siphons of *Transennella tantilla* are split along one half their length (Fig. 4). Tentacles are also present on the distal end of the incurrent and excurrent siphons, with the number on the incurrent siphon varying from 9-12 and the number on the excurrent siphon varying from 10-14. Brian Stagl (pers. comm.) found a slight correlation between the size of the

specimen and the number of siphonal tentacles, but no significant difference between the number of tentacles present on each species. The tentacles on the incurrent siphon are longer and more slender than those of *T. confusa*, and bend to form a sieve-like network when the animal is pumping water. This network functions to strain out large particles before they can enter the mantle cavity. Ansell (1961) noted this type of function for other Veneracea.

The siphonal tentacles of *Transennella tantilla* are either non-pigmented or have a light yellow coloration at the tips. A brown pigment is found at the base of each tentacle and lining the siphon split. The body of the siphon is translucent with an occasional yellow or white patch. When the siphons are fully extended in a living animal, there is an angle of divergence of approximately 40° between the tips.

Both species of *Transennella* have a valvular membrane at the distal end of the excurrent siphon, and the surrounding tentacles are smaller than those of the incurrent siphon. When the animals first begin to pump water, the siphons slowly extend from the shell, and then the valvular membrane pops out. The distal end of the siphon is capable of contraction and this may aid in the expulsion of the valvular membrane. Ansell (1961) proposed that the function of the valvular membrane is that of confining and directing the exhalant current.

At the proximal end of the siphons of both species there are valve-like structures, the siphonal membranes. The excurrent siphonal membrane has a vertical, slit-like opening, while the incurrent siphonal membrane has a larger, more ovate opening. Both sets of siphonal membranes are capable of closing completely, which effectively halts water movement through the animal. Sellmer (1967) described and discussed these membranes in *Gemma gemma*.

Digestive system

The general morphology of the alimentary canal of both species of *Transennella* was examined in preserved specimens. The mouth is posterior to the anterior adductor muscle and is bordered by the labial palps. The mouth opens ventrally and enters a short esophagus which is surrounded by digestive diverticula. The esophagus rises dorsally and then turns posteriorly to enter the stomach.

The stomach lies in the antero-dorsal plane of the visceral mass and is surrounded by digestive diverticula. Due to the small size of the stomach, stomach function was not observed (see Narchi, 1971, for a description of stomach function in *Transennella tantilla*). Both species have the same stomach morphology. The stomach is of Type V as defined by Purchon (1960), but it is simplified with fewer sorting folds and a reduced dorsal pouch. A translucent cuticle layer, the gastric shield, is found on the postero-dorsal wall of the stomach. Anterior to the gastric shield is the dorsal hood. The digestive diverticula enter the stomach in two places: the right caecum which opens into the stomach just ventral to the esophagus, and the left caecum which opens into the antero-ventral wall of the stomach.

The midgut, which consists of the combined style sac-intestine, connects with the posterior ventral wall of the stomach. The midgut passes ventrally to the foot. The intestine starts at the ventral end of the midgut and then turns anteriorly. In *Transennella confusa*, the intestine forms a tight coil under the stomach (Fig. 5), while in *T. tantilla* it forms a short loop (Fig. 6) or, infrequently, a small coil. The intestine then proceeds posteriorly beyond the stomach, ascends through the gonad to the level of the pericardial cavity, where it penetrates the ventricle. It then continues posteriorly, passing over the dorsal side of the posterior adductor muscle to end in the anal papillae on the ventral side of the posterior adductor muscle.

The difference in intestinal shape and length between the two species may be related to feeding behavior. Purchon (1971) cited studies that show that the midgut and intestine are sites of digestion, as well as being areas of water absorption and consolidation of fecal material. Based on the morphology and observed function of the siphons, *Transennella confusa* is less selective in feeding than is *T. tantilla*. *T. confusa* would require a larger area of digestion and fecal compaction since more material (including more non-nutritive material) would be collected by the animal.

ECOLOGY AND NATURAL HISTORY

The northeastern Pacific species of *Transennella* usually inhabit protected bays, although they are occasionally found on the open coast in beds of the marine grass *Phyllospadix*. The animals lie within the first few centimeters of the substrate and are very active burrowers if dislodged. Their depth distribution ranges from low intertidal to a subtidal depth of 50 m for *T. confusa*, and from middle intertidal to a subtidal depth of 10 m for *T. tantilla*. In subtidal samples from south of San Francisco Bay, *T. confusa* is found in greater numbers than is *T. tantilla*.

In all of the sampling sites, except one, the sediment was composed of sandy mud. The sediment of Princeton Harbor, San Mateo County, where *Transennella confusa* occurs without *T. tantilla*, consists of coarse gravel and sand. Maurer (1968) found the size and distribution of *T. tantilla* relatively unaffected by sediment particle size, but he did not sample any areas that contained gravel.

Both species of *Transennella* brood their young inside the inner demibranch, and brood-carrying individuals may be found at any time of the year. Monthly sampling showed an increase in brood-carrying females and ripe males in early spring (May-June) for *T. tantilla* and in midsummer (July-August) for *T. confusa* (Gray, 1978), although there was some overlap. Brooded young always have the same shell pigmentation as that of the brooding adult. An examination of the electrophoretic properties of the enzymes associated with the digestive system shows no overlap between the species in the isozymes for both adults and brooded young (Bill Rotz, pers. comm.).

Hansen (1953) found evidence of protandrous hermaphroditism in a population of *Transennella tantilla* from False Bay, Washington. He noted that sex reversal occurred at the shell length of 4 mm. Direct evidence of protandrous hermaphroditism for *T. confusa* was not observed in this study, possibly due to sampling size, but males greater than 5.5 mm in shell length occasionally were found in the Tomales Bay population.

Populations of *Transennella* from Tomales Bay are infected with the sporocysts and metacercaria of the trematode *Pavatrema*. The clams are double intermediate hosts for the parasite, with the sporocysts entering the clam and attaching to the gonad. The sporocysts undergo maturation, and appear to castrate the clam in the process, since the gonads of parasitized clams are degenerate and show little signs of gamete development. The mature sporocysts release cercaria into the water, which then re-infect the clams and develop into metacercaria, forming pits on the inside of the shell (Kaufman & Zeitlin, 1971). The final host for the trematode is probably one of the many shorebirds in the area (Doug Yasumura, pers. comm.). Both species have exhibited evidence of infection.

Predators of *Transennella* include shorebirds and crabs. Drilled valves occasionally may be found, indicating predation by one or more of the mud flat gastropods.

The species co-occur at three locations in California (Tomales Bay and Bolinas Lagoon, Marin County, and Bodega Bay, Sonoma County) and one location in Oregon (Coos Bay). Subtidal collections in central San Francisco Bay contain only *Transennella confusa*, as do intertidal collections in Princeton Harbor, San Mateo County. Museum collections have specimens of *T. tantilla* ranging from southeastern Alaska to Cabo San Lucas, Baja California, and the northern end of the Gulf of California (Fig. 14). No specimens of *T. confusa* have been found in collections from north of Coos Bay, Oregon, and it is found only in subtidal samples south of Princeton Harbor, San Mateo County, California.

CONCLUSIONS

Differences in the shell and internal morphology indicate the presence of two distinct species of *Transennella* in the northeastern Pacific. There are also some variations in depth

distribution and sediment preference between the two species. The currently known range of *T. confusa* may be extended as more subtidal material is examined, since its occurrence in central California, south of Princeton Harbor, has been documented only in off-shore samples.

Further work on the physiology, ecology and reproductive biology of *Transennella confusa* would be beneficial in order to quantify observed trends, and in clarifying previous work on *T. tantilla* that did not take into account the presence of a second, sympatric species.

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EFFECTS OF POPULATION DENSITY AND SUBSTRATUM TYPE ON GROWTH AND MIGRATION OF *ELLIPTIO COMPLANATA* (BIVALVIA: UNIONIDAE)

Pieter W. Kat

ABSTRACT

Results gathered in this manipulation experiment suggest that much of unionid ecology needs to be re-evaluated. A unionid species such as *Elliptio complanata* may well be encountered on a number of different substrata, but growth rate of the individuals in each microhabitat can be statistically different. Density of assemblages also can affect growth rates, and certainly influences rates of migration. The potential for spatial competition for high quality microhabitats thus can be high, depending on standing crop of unionids in the body of water and on site availability. Small individuals actively migrate and can be carried large distances by currents. Such distances might approximate dispersal distances by glochidial hosts. Differential rates of growth in various microhabitats could account for some of the skewedness of size-frequency plots of unionid assemblages: similar-sized individuals could be variously aged.

INTRODUCTION

Ecological studies of bivalves of the family Unionidae remain limited, despite their recognized importance as a major component of the aquatic benthos. Researchers have chosen instead to concentrate on faunal distribution, physiology and taxonomy, with the result that large portions of unionid life history remain unknown. For instance, it frequently has been observed that juvenile unionids are rarely encountered in adult habitats (Matteson, 1948, 1955; Negus, 1966; Cvancara, 1972; Fisher & Tevesz, 1976), and, as a result, size-frequency plots based on collections are often skewed to the right, with a single age class consisting of large individuals dominating the assemblage. Interpretations of this phenomenon generally have included exceptional recruitment during a single, particularly benign, period, high levels of selective predation on juvenile bivalves, and the possibility that juveniles have very different habitat preferences than those of adults (e.g., Ökland, 1963; Negus, 1966; Fisher & Tevesz, 1976).

Substratum preference among unionids also remains poorly understood. Some authors mention that substratum type is important in regulating distribution (Isely, 1914; Negus, 1966; Moyle & Bacon, 1969; Johnson, 1970; Harman, 1972; Clarke, 1973; Fuller, 1974; Haukioja & Hakala, 1974; Fisher & Tevesz, 1976), while others observe that bottom type is of secondary importance in some habitats (Cvancara & Harrison, 1965; Cvancara, 1972). It is clear that, in general, freshwater bivalves are less substratum-specific than are their marine counterparts, but the reasons for this reduced specificity are not fully understood (Tevesz & McCall, 1979). The large degree of phenotypic plasticity common among unionids may allow modification of form to suit substratum type (as in the "lake" and "river" forms of *Anodonta cataracta* Say), but it is uncertain whether there are fitness consequences associated with substratum selection or whether there is a substratum type in which growth, survival and reproduction are optimal for a given species. There are indications that muddy substrata are either inimical to, or at least reduce, growth of unionids (Matteson, 1948; Stansbery, 1967; Haukioja & Hakala, 1974; Fisher & Tevesz, 1976), but these observations are countered by other authors who find unionids in abundance on muddy substrata (Cvancara, 1972; Tevesz & McCall, 1979). Occurrence on a substratum type does not indicate preference, however;

the ecology of unionids remains so obscure that it is not known whether there is any level of selectivity for habitat type. As a consequence, it is uncertain whether there is any level of competition for space among unionids in lotic habitats; if all substrata are equally acceptable, levels of competition should be extremely low.

Knowledge of the processes of dispersal and migration in streams is also poor. Isely (1911) observed that juvenile unionids disperse from certain areas within streams to colonize the rest of the habitat, and that adults move little if at all (Isely, 1914). These conclusions are refuted by data from long-term studies which indicate considerable fluctuation in community composition and population densities, indicating a large degree of mobility of adults (Van Cleave, 1940; Negus, 1966). Predation is not implicated in these fluctuations.

It was the purpose of this study to document the effects of different substrata on growth rates of natural populations of *Elliptio complanata* (Lightfoot), as well as to document rates of migration as influenced by sediment type and density of the assemblage in a lotic habitat.

METHODS

Norwich Creek in Talbot County, Maryland, was selected as the study site for a number of reasons. The stream is rather small, generally no more than 3 m wide, and therefore easy to sample. Nevertheless, it exhibits a wide variety of bottom types ranging from gravel to mud. Water depth averages about 1 m, but may reach 2-2.5 m in small depressions. Water level may increase by as much as 1.5 m during floods. The stream, though it flows through predominantly agricultural areas, is relatively undisturbed and contains one of the richest unionid faunas on the Delmarva peninsula. Table 1 lists species present and their densities. Norwich Creek is part of the Tuckahoe River drainage.

On 10 May 1979, a total of 294 *Elliptio complanata* was marked with Roman numerals filed into the shell to identify stations and individuals. Length, width and height of each individual was measured, after which they were re-inserted into the substratum. The stations measured 2 m long by 1 m wide and were marked with six stakes to divide each into two replicates of 1 m^2 (Fig. 1). All other bivalves were removed from the stations and transplanted downstream from station 1. Wherever possible, individuals of *E. complanata* to be used in the experiment were taken from the station site itself, or from identical substrata. Bivalves were re-inserted in a non-random fashion imitating natural distribution patterns: highest densities in shallow water, next to logs, rocks, etc. The stations were not caged in any way because of the difficulty of maintaining cages in lotic environments subject to wide variations in flow rates and water levels (Isely, 1914). The experimental design is presented in Table 2.

The site was revisited on 10 July 1980. Each station was sampled to recover marked individuals which were counted and measured. All immigrants also were counted and measured. In addition, the areas between stations were sampled in an attempt to recover marked individuals missing from their original sites. Voucher specimens were deposited in the collections of the Academy of Natural Sciences of Philadelphia.

TABLE 1. Unionid species and their densities in Norwich Creek.

Species	Density
Elliptio complanata	20 - 15/m^2
Elliptio lanceolata (Lea)	1 - 0.5/m^2
Anodonta cataracta	1 - 0.5/m^2
Alasmidonta heterodon (Lea)	1 - 0.5/m^2
Strophitus undulatus (Say)	1 - 0.5/m^2
Alasmidonta undulata (Say)	0.2 - 0.1/m^2
Lampsilis radiata (Gmelin)	0.2 - 0.1/m^2
Ligumia nasuta (Say)	0.2 - 0.1/m^2

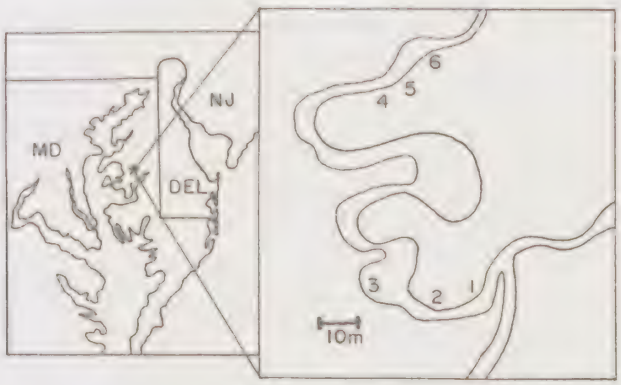

FIG. 1. Location of Norwich Creek and sample stations. Current flows from top to bottom. DEL = Delaware; MD = Maryland; NJ = New Jersey, U.S.A.

TABLE 2. Substratum type and *Elliptio complanata* densities at the experimental stations.

Station	Substratum type	Density
1	Sand/gravel/clay	2x: 30/m^2, two replicates
2	Sand/gravel/clay	4x: 60/m^2, two replicates
3A	Mud/clay	2x: 30/m^2, one replicate
3B	Mud/clay	1x: 15/m^2, two replicates
4	Sand/gravel/clay	1x: 15/m^2, two replicates
5	Sand/gravel/clay	1/2x: 8/m^2, two replicates
6	Sand/gravel/clay	1/4x: 4/m^2, two replicates

RESULTS

Density effects on growth

Low initial availability as well as differential rates of migration of small individuals limited comparisons of growth to bivalves between 80 and 100 mm. Growth is presented as average increase in length in millimeters (Table 3); increments in width might be sex-related and are not presented; and increments in height contained errors in placement of calipers on the shell and also are not considered. One-way analysis of variance results (Table 4) show that there are significant effects of bivalve density on growth rate: growth increments are greater for each size class at the normal and 1/2x densities than at 2x and 4x densities. A note of caution must be added to interpretation of these results since sample sizes were often small, especially at stations 4 and 5, and the difference in growth rate observed should be taken as a suggestion rather than a distinct pattern. Also, density of the bivalves was not rigorously controlled during the experiment; many tagged individuals migrated away from the station sites, and, although some were replaced by immigrants, there is no guarantee that migration and immigration occurred at the same rate to give a uniform density. This was certainly not the case at station 2, where density was reduced from 60 individuals/m^2 in 1979 to 15.5/m^2 in 1980.

TABLE 3. Mean increase (in mm) in length of *Elliptio complanata* at each station.

Initial size (Length in mm)	Station						
	1	2	3A	3B	4	5	6
60-64	9.4 (1)*	–	–	10.1 (2)	–	–	–
65-69	6.3 (1)	–	6.6 (1)	6.1 (1)	6.0 (2)	–	–
70-74	4.2 (1)	–	4.2 (2)	4.0 (3)	3.9 (2)	4.6 (2)	4.8 (1)
75-79	3.3 (2)	–	2.6 (2)	2.7 (2)	3.7 (2)	–	3.6 (2)
80-84	1.2 (7)	1.3 (6)	0.6 (4)	0.6 (4)	–	1.6 (1)	1.4 (1)
85-89	1.0 (17)	1.1 (10)	0.5 (8)	0.4 (6)	1.6 (8)	1.4 (4)	1.5 (1)
>90	0.6 (12)	0.6 (20)	0.2 (6)	0.2 (7)	1.1 (7)	1.1 (6)	1.1 (1)

*Numbers in parentheses indicate sample size.

Substratum effect on growth

Comparisons were made between growth at twice normal density (1 and 3A) and normal density (3B and 4) stations. Results and statistical tests are presented in Table 4. It is clear that substratum type has a highly significant effect on growth rate of *Elliptio complanata* which is especially manifested at higher densities.

Individuals ranging from 60-74 mm in length appear not to show any effects of density or substratum type on growth rate, but these findings might be artifacts of small sample sizes.

TABLE 4. Analysis of variance results for density and substratum effects on growth of *Elliptio complanata*.

Bivalve size (mm)	Treatment	F	Significance level
80-84	Density effects	7.858	.01
85-89	Density effects	4.431	.01
>90	Density effects	5.967	.01
80-95	Substratum effects (1x)	21.309	.001
80-95	Substratum effects (2x)	45.793	.001

F = the variance ratio.

Density effects on migration (stations 1, 2, 4, 5, 6)

Results of the migration study are presented in Table 5. In general, recovery rates were lower than expected, especially at the control station (4) and the low density stations 5 and 6. Percent recovery at station 2 is statistically significantly different from percent recovery at all other stations; this finding is largely attributable to high initial densities. It is also the only station from which individuals migrated *upstream*, and the station where members of the assemblage migrated furthest away (up to 15 m).

TABLE 5. Recovery, immigration and migration of *Elliptio complanata* at all stations.

Factors measured	Station						
	1	2	3A	3B	4	5	6
Initial density	30/m²	60/m²	30/m²	15/m²	15/m²	8/m²	4/m²
Substratum type*	S	S	M	M	S	S	S
% recovered at site	68	13	66	76	66	69	75
No. migrated 1-5 m	–	8	4	3	–	2	1
No. migrated 5-10 m	–	5	–	–	–	–	–
No. migrated >10 m	–	3	–	–	–	–	–
Total % recovered	68	30	80	86	70	81	88
No. immigrants	23	13	19	14	15	22	27
Final density	32/m²	16/m²	33/m²	18/m²	17/m²	24/m²	17/m²

*Substratum type: S = sand/gravel/clay mix; M = mud/clay mix.

Substratum effects on migration (stations 1, 3A, 3B, 4)

Muddy stations (3A and 3B) had higher percentages of total recovery than sandy stations (1, 2, 4-6) (Table 5). These data serve to emphasize the effects of current as well as substratum on migration; station 3 had sluggish currents, as it was located away from the main channel, and thus only received countercurrent flow. Migrating individuals therefore must rely on their own efforts to move. Immigrants into this area were probably deposited during floods.

Effects of size on migration

Small *Elliptio complanata* in this stream had almost three-fold higher rates of migration (as measured by percent loss from each station) than large individuals (Table 6). The only stations which showed any statistically significant reduction of this trend were the muddy

TABLE 6. Migration rates: percent of original individuals in size class that migrated from station.

Station	Size class (mm)			
	<50	50-69	70-90	>90
1	100	92	33	20
2	–	100	57	38
3	–	63	15	20
4	100	100	30	0
5	–	100	23	15
6	–	100	20	15
Average	100	92.5	29	18

stations, 3A and 3B. Nevertheless, out of seven individuals which had migrated out of this area, five measured less than 69 mm. Large individuals also migrated, however, especially out of such high density conditions as station 2. Out of three individuals which had migrated more than 10 m away from station 2, two measured over 90 mm in length. None of the smaller individuals missing from station 2 were recovered in subsequent searches covering a distance of 15 m downstream.

Table 7 presents composite migration rates of immigrants into all the experimental stations. From this table, it seems that two size classes are most active in migration: 60-69 and 80-89 mm. This is somewhat misleading, however, since the Norwich Creek assemblage is dominated by individuals between 80-89 mm; hence any dispersal, active or passive, would tend to be dominated by this size class. When the figures are corrected for relative densities, a more meaningful rate of dispersal shows the smaller size classes most active, followed by a decline in activity of larger individuals.

TABLE 7. Composite migration rates and computation of corrected migration rates of *Elliptio complanata* into the experimental stations.

Composite factors	Size class (mm)					
	40-49	50-59	60-69	70-79	80-89	>90
a. % of immigrants	4.10	12.10	27.40	11.60	32.90	11.60
b. % of total population	3.60	5.90	10.70	15.50	41.70	22.60
c. corrected frequency (a/b)	1.14	2.08	2.56	0.75	0.79	0.51
d. corrected migration rate*	14.50	26.50	32.60	9.50	10.70	6.30

*% of summation of corrected frequencies.

DISCUSSION

Data gathered in this study suggest that substratum type has profound effects on the growth rate of *Elliptio complanata*. While bivalves were almost equally numerous under natural conditions in a sand/gravel/clay mix and muds, growth data reveal that muddy substrata reduce growth rate, at least in large individuals. While substratum type has been known to affect growth rate of marine bivalves (Pratt, 1953; Sanders, 1958; Driscoll & Brandon, 1973), it has not been documented previously for unionids.

Possible reasons for this reduction in growth rate are numerous and can involve unusual energy demands, which reduce the total amount of energy available for growth. For example, fine sediments in suspension are notorious for clogging filtration systems of bivalves and thereby reducing feeding efficiency (Headlee, 1906; Ellis, 1936; Purchon, 1968). Also, soft substrata require an almost constant energy expenditure to retain position within the sediments. (I disagree with Fisher & Tevesz (1976) that *Elliptio complanata* is unable to maintain position in soft sediments; I have collected individuals from knee-deep, soupy muds, but all specimens had their foot extruded and probably had to make frequent adjustments to keep from sinking below the sediment surface.) Finally, individuals collected from muds often exhibit signs of irritation of the mantle, with subsequent secretion of nacre in the form of blisters, pustules or pearls (Baker, 1928).

It could be argued that substratum type is merely a consequence of current strength, and

that it is not soft substrata which reduce growth, but the associated weak currents which supply less nutritive material. Current strength and food supply, for example, have been implicated as a cause of intraspecific size variability for a number of species (Ortmann, 1913). Cause and effect are difficult to separate in this case, but similarity of growth rates of small individuals (non-significant differences) in sandy and muddy substrata present some evidence against nutrition-related stress. Significant reduction of growth rate does not begin to appear until the bivalves reached a length of 75 mm. Reasons for this trend could be the uniformly high activity rate of small bivalves regardless of substratum type, as well as increased weight of large shells, which then require more frequent position adjustments in soft substrata.

Density of the assemblage may well have had an effect on growth rate and certainly influenced rates of migration. Migration from areas of high density was common and involved up to 87% of the population at the highest density station.

These results disagree to some extent with a similar study performed by Isely (1914). His results indicate very low migration rates (85% recovery) for several species of *Quadrula*. Species such as *Anodonta grandis* Say had higher rates of migration (45% recovery), and it might be that activity levels vary from species to species. Isely (1914) does, however, point out that occurrence of a species on a certain substratum might be by chance rather than choice. This study indicates that, while *Elliptio complanata* occurs on a number of substrata, fitness consequences of that distribution are not necessarily equal; since growth rates are reduced in muddy substrata, reproductive effort also might be. Certainly reduced growth rates would result in smaller individuals, with concomitant reduction in fecundity.

The stream habitat thus can be divided into a number of high and low quality microhabitats. High quality microhabitats are characterized by stable substrata, uncrowded conditions and protection from scour. Low quality microhabitats would include those with unstable substrata (definition of an unstable substratum might differ for each species; soft muds are not necessarily unstable for thin-shelled species such as *Villosa* and *Anodonta*) and those in which there is a significant reduction of energy available for growth and reproduction. If occurrence of high-quality microhabitats is infrequent within the average dispersal distance of a juvenile unionid, and/or if adult density is high in a given stream, the potential for both intra- and interspecific interaction is created. Low-quality microhabitats (such as those with muddy substrata for *Elliptio complanata*) are not necessarily inimical to survival of individuals, which may migrate out of these habitats by active or passive dispersal by currents. The latter means of migration, however, does not guarantee amelioration of microhabitat; in fact, it is common to see unionids washed up on banks after floods, and muddy areas probably serve as sinks for passively dispersing individuals because of the reduction of current associated with them.

Elliptio complanata is demonstrated to have high rates of migration, and it is conceivable that individuals experience a number of microhabitats during their lifetimes. Since growth rates of large bivalves are different in various substrata, the ratio of good to bad microhabitats experienced may, to a large extent, determine size of an individual. Therefore, skewedness of size-frequency plots may not indicate dominance of a certain large age class, but of a size class composed of differently aged individuals.

It generally has been assumed that glochidial hosts are responsible for long-distance dispersal of unionids (e.g., Fuller, 1974). This may well be true if unionids time the release of glochidia to correspond with spawning or winter migrations of their fish hosts, or if fish hosts disperse unionids between drainages during floods, etc. However, many freshwater fish restrict their movements and become territorial after such migrations (Gerking, 1959; Horwitz, 1978). *Elliptio complanata* females in Norwich Creek had fully formed glochidia in their demibranchs on July 10, so that discharge was imminent (Matteson, 1948). The host fish, *Perca flavescens*, is in all probability limited to short-distance feeding movements during July and August (Allen, 1935), so that dispersal distance of active unionids such as *E. complanata*

by their fish host is likely to be on the same order as that achieved by bivalves dispersing from such juvenile microhabitats as riffles (Isely, 1911) to high quality adult habitats.

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SHELL DISSOLUTION AS A SIGNIFICANT CAUSE OF MORTALITY FOR *CORBICULA FLUMINEA* (BIVALVIA: CORBICULIDAE) INHABITING ACIDIC WATERS

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ABSTRACT

Dissolution of the shell in the umbonal region is a major source of mortality for *Corbicula fluminea* inhabiting acidic waters. Resistance to similar dissolution among the Unionidae may be explained in part by greater rates of compensatory nacre deposition, but seems to occur primarily because of the presence of thick conchiolin layers within the shell.

INTRODUCTION

Corbicula fluminea (Müller 1774) has gained considerable notoriety as one of the most successful introduced species of mollusk, having spread across a wide geographic range in a short time, and building up populations of up to 25,000 individuals per sq ft (juveniles ?) along the way (Sinclair, 1971). Although *Corbicula* has some natural vertebrate predators (Britton & Murphy, 1977), increases in geographic range and population numbers seem to continue unabated, causing widespread concern about the effect of this invasion on native aquatic bivalves. Although direct evidence has not been presented to support claims of spatial competition between *Corbicula* and autochthonous bivalves, competitive interactions are inferred since increases in population size of this genus are usually accompanied by decreases in unionid populations (Fuller & Imlay, 1976; Gardener et al., 1976; Fuller & Richardson, 1977). An alternative explanation of this "competitive" effect may be suggested by the observation that *Corbicula* can tolerate the ubiquitously deteriorating environmental conditions of aquatic habitats better than can unionids (Habel, 1970; Diaz, 1974; Kraemer, 1976; Horne & McIntosh, 1979) and hence increase in relative abundance (Kraemer, 1979). *Corbicula* seems to be exhibiting the classic exponential population increase characteristic of species introduced into essentially open habitats (from which unionids have been or are being excluded). Interestingly, some populations seem to be experiencing drastic fluctuations in population numbers which also has followed such logistic growth in both laboratory and natural single species assemblages (Murie, 1934; Hickie, 1936; Sinclair & Isom, 1963; Horning & Keup, 1964; Bickel, 1966; Krebs, 1972; Sickel & Heyn, 1980).

Personal observations, however, indicate that *Corbicula* does not always establish numerical superiority over unionid populations where they co-occur, even in areas where *Corbicula* has been established for a number of years (e.g., branches of the Ocmulgee River, Georgia; branches of the Suwannee River, Florida; Lake Waccamaw, North Carolina; see also Kraemer, 1979). One habitat type where abundances of *Corbicula* are consistently below those of unionids can be characterized by both low pH of the water and low levels of habitat disturbance. It is the purpose of this paper to document shell dissolution as a major source of mortality for *Corbicula* inhabiting such acidic waters.

METHODS

Corbicula specimens were collected on January 10, 1980, from Mosquito Creek below the Florida State Hospital dam, Chattahoochee, Gadsden Co., Florida. This site, although relatively disturbed, was

was chosen because of the ease by which living and dead specimens of *Corbicula* could be collected. The bottom was composed of a sand/clay mix with bare rock in areas of scour. Water depth varied from 0.3 to 0.8 m, and the current was approximately 0.4 m/sec. The pH of the water was 5.6 at the time of sampling. Densities of *Corbicula* were locally very high, especially in depressions in the stream bottom, where the bivalves occurred in a layer 7-10 cm above the substratum in densities of approximately 580/m^2. The unionid assemblage, consisting mainly of *Elliptio arctata* (Conrad 1834), with some *Carunculina parva* (Barnes 1823) and *E. icterina* (Conrad 1834), was characterized by much lower densities, on the order of 2-5 individuals/m^2. Extent of shell dissolution on these unionids was not different from that occurring in other moderately acidic habitats. Specimens of *E. complanata* (Lightfoot 1786) exhibiting similar amounts of shell dissolution were used for comparative purposes in this study, and were collected from branches of the Chester River, Kent Co., Maryland. Voucher specimens of the species used in this study have been deposited in the collections of the Academy of Natural Sciences of Philadelphia.

Shells were embedded in clear plastic, sectioned, polished with carborundum and diamond grit, and acid etched (5% HCl) for Scanning Electron Microscopy. Histological examinations were performed on five *Corbicula* specimens ranging in size from 20-25 mm which showed evidence of recent shell dissolution but were still alive. These bivalves carefully were excised from their shells, fixed in 10% formalin (for 24 hr), embedded in paraffin, sectioned at 6 μm, stained with Harris hematoxylin, and counterstained with eosin Y.

RESULTS

Shell dissolution in *Corbicula fluminea* from Mosquito Creek is restricted to the umbonal regions of the shell where the periostracum has worn off. Holes eventually appear in the umbo as a result of this dissolution, but bivalves with intact shells in advanced stages of dissolution showed a number of other associated effects, including breakage and weakening of the ligament and dissolution of dentition (Fig. 1A). It is probable that these associated effects are sublethal since they negatively affect normal functioning of the shell.

Size-frequency diagrams of valves of living and dead bivalves show five peaks which correspond well to age classes suggested by previous authors (Sinclair & Isom, 1963; Gardener et al., 1976) (Fig. 2). While bivalves in the first two size classes often showed signs of some dissolution in the umbonal region, complete dissolution was not observed before the bivalves attained a minimum shell length of about 22 mm, which corresponds to an age of about three years (complete umbonal dissolution may well have occurred before this: small empty shells probably are differentially transported by the fast current). Frequency of complete dissolution increases in the fourth size class, and few bivalves in the fifth size class remain alive. Life expectancy of *Corbicula* is thus limited to a maximum of five years, with probable debilitating sublethal effects appearing in the first and second years. Of the 150 articulated valves of dead specimens examined, only 4% did not show complete umbonal dissolution and are presumed to have died from other causes.

Histological examination of mantle tissues of live individuals in which complete umbonal dissolution had occurred revealed the pathological effects of shell dissolution (Fig. 1D). The mantle generally had ruptured, and cells composing the mantle were necrotic, often showing signs of cell wall disintegration and pycnotic nuclei. Amoebocytes were common among the mantle cells. Tissues underlying the mantle showed similar pathological effects, and massed amoebocytes were common. It is assumed that the bivalves are attempting to cope with an invasion of microorganisms following shell dissolution, but absence of any shell repair in other animals with similar umbonal dissolution make it clear that the animals will not be able to counter the effects of such an invasion.

Scanning Electron Microscope (SEM) examination of *Corbicula fluminea* revealed a shell composed entirely of complex cross lamellar crystals. Counts & Prezant (1979) mentioned that the periostracum is tightly bonded to the shell by a rugose inner surface, but shell dissolution appears to proceed rapidly where the periostracum is worn away: once a small hole is formed in the periostracum, a pit rapidly forms underneath it and further loosens the periostracum from below (Fig. 1C). Organic layers (conchiolin) are narrow (Counts & Prezant, 1979).

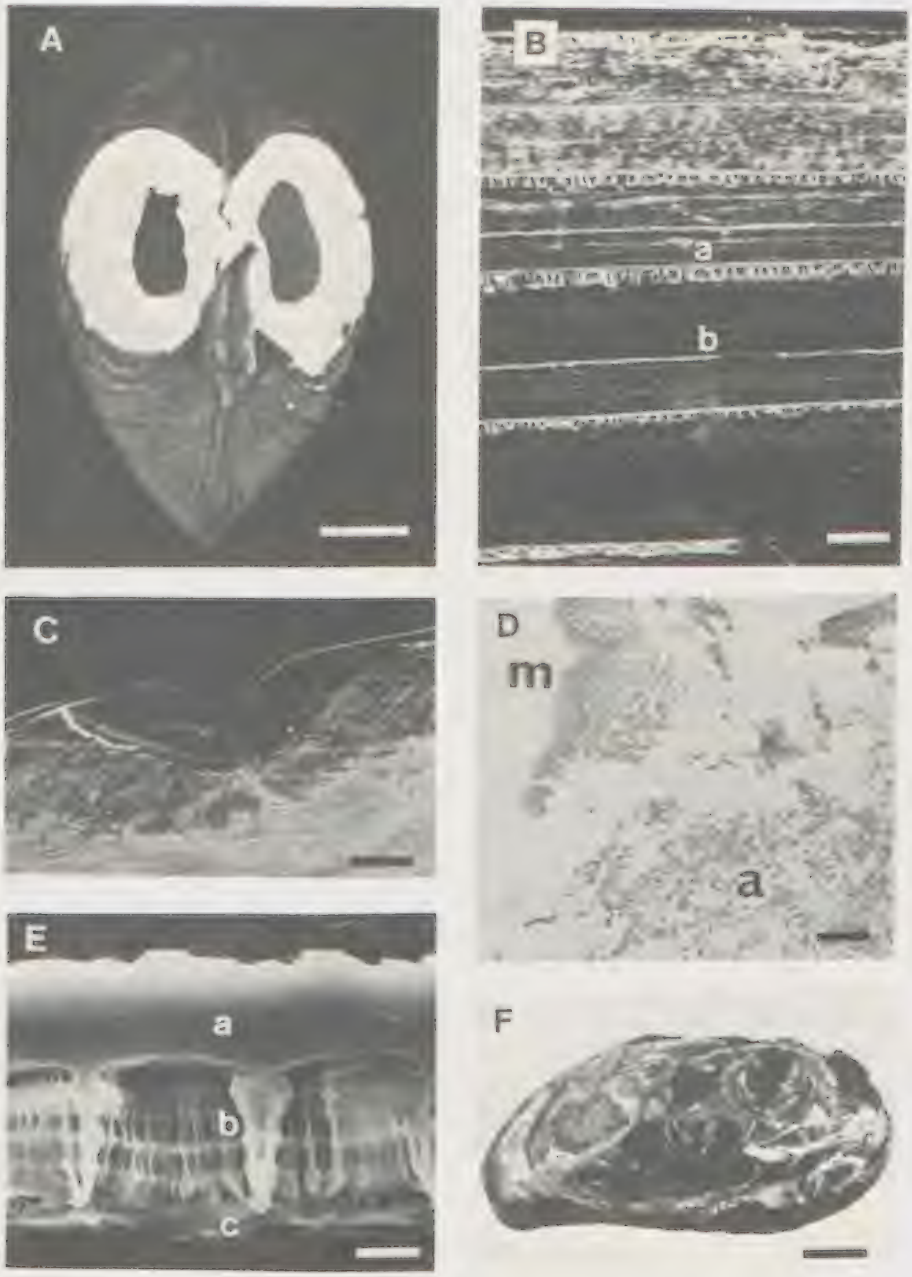

FIG. 1. A, Complete dissolution of the umbonal region in *Corbicula*, with breakage of the ligament and dissolution of dentition. Scale bar = 5 mm. B, Scanning electron microscope (SEM) photograph of the nacre of *Elliptio complanata*, showing thick conchiolin layers (a) alternating with thinner bands (b). Dissolution has loosened the uppermost conchiolin layers; a partial layer can be seen at bottom left. Scale bar = 200 μ. C, SEM photograph of the shell of *Corbicula* showing pits forming in the area where the periostracum has worn away (top). Scale bar = 200 μ. D, Effects of complete dissolution on the mantle and underlying tissues in *Corbicula*. The mantle (m) is necrotic, and massed amoebocytes (a) are common. Scale bar = 100 μ, specimen size = 23 mm. E, SEM photograph of the thick conchiolin layer of *E. complanata*. Note the structure of the reticulate band (b), and the rugose surfaces of the upper and lower homogeneous bands in contact with the nacre (a and c). Scale bar = 5 μ. F, Extensively dissolved specimen of *E. complanata* from Newville Lake, Halfway River East, Cumberland Co., Nova Scotia. Dark areas on the shell are successive organic layers protecting the underlying nacre. Scale bar = 2 cm.

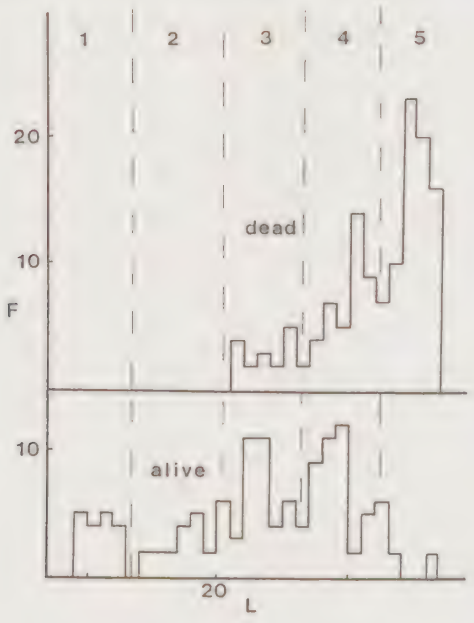

FIG. 2. Size frequency diagram of dead and living specimens of *Corbicula* collected from Mosquito Creek. Dashed lines indicate approximate age classes; shell length (L) is in mm.

A similar SEM examination of the shell of *Elliptio complanata* revealed a shell of different structure composed of aragonitic prismatic and laminar crystals. Thick conchiolin layers are common, and each consists of three separate bands (Fig. 1B). The upper band is composed of a rather thick (9 μm) homogeneous layer of conchiolin with a rugose upper surface, which is in contact with the laminar crystals forming the nacre (Fig. 1E). Below this lies a reticulate band (± 10 μm thick) composed of tightly packed, dagger-shaped laminae which seem to enclose rounded chambers (Fig. 1E). The bottom of the conchiolin layer is composed of another, thinner sheet of conchiolin measuring about 1-2 μm in thickness. This band also exhibits a rugose surface where it comes in contact with the nacre. It is probable that the reticulate portions of the conchiolin layer contain calcareous structures which dissolved away when the specimen was etched with HCl. Thick conchiolin layers seem to alternate with thinner layers composed of homogeneous sheets, and may end rather abruptly (Fig. 1B). It may well be that the microstructure of these conchiolin layers can be used as a taxonomic character.

DISCUSSION

Dissolution of shell in the umbonal region is a major source of mortality for *Corbicula fluminea* inhabiting the acidic waters of Mosquito Creek. Debilitating associated effects such as breakage of the ligament and dissolution of dentition occur before complete dissolution of the umbo. Mortality presumably results from an invasion of microorganisms.

Personal observations indicate that unionids in similar environments rarely suffer mortality from shell dissolution except at an advanced age. Extensive shell dissolution can take place (Fig. 1F) without lethal effects, even though ligament and dentition functions are adversely affected as in *Corbicula*. Breakage of extensively dissolved shell usually occurs in the area of the adductor muscles, possibly as a result of excessive strain imposed on the thin

shell layers. Resistance to shell dissolution may be explained in part by greater rates of compensatory nacre deposition on the inner surface of the unionid shell, but seems to occur primarily because of the existence of thick conchiolin layers within the shell.

While the existence of these and similar layers in the Unionidae has been documented for some time (e.g., Gray, 1833; Tolstikova, 1974), their function has remained obscure. Tevesz & Carter (1980: 315-316) have termed them "adventitious conchiolin layers" and mentioned that they occur sporadically through the nacre in the umbonal region, but they are uncertain as to what actuates their formation. These layers also exhibit remarkable convergence with the conchiolin layers described for the Corbulidae (Lewy & Samtleben, 1979), in which they are hypothesized to deter boring as well as shell dissolution. While unionids do not have to cope with predatory boring gastropods, any unionid shell which exhibits extensive dissolution reveals successive calcareous layers protected by these organic sheets (Fig. 1F). Unlike *Corbicula*, once the unionid periostracum has worn away, shell dissolution in similar acidic waters may be sufficiently retarded by these conchiolin layers to permit compensatory shell deposition, depending on environmental conditions. Unionids probably will be excluded from very low pH conditions not only due to rapid rates of shell dissolution, but also because of the difficulty of concentrating calcium carbonate under those conditions (see also a discussion of the other effects of low pH on unionids in Fuller, 1974).

Members of the family Corbiculidae have a much shorter evolutionary history in aquatic habitats than unionids: fossil forms are fully marine, and some Recent species are restricted to brackish water (Moore, 1969). Kraemer (1979) found *Corbicula* conservative in a number of characters, mentioned that unionids are better adapted to river life, and doubted that *Corbicula* can outcompete unionids in undisturbed environments. (A disturbed environment generally can be defined as one in which ecological conditions have been modified by human activities, including introduction of pollutants, increases in sediment loads, maintenance dredging of shoals, bank stabilization projects, constructions of dams, etc.) The results of this study indicate that the conchiolin layers in unionid shells might be adaptive in that they retard rates of shell dissolution in lotic habitats of low pH. However, early reproduction, viviparity, possible self-fertilization (McLeod & Sailstad, 1980) and a simpler life cycle than found among unionids characterize *Corbicula* as an opportunistic species capable of rapid colonizations and population buildups. This led Gardener et al. (1976), among others, to express concern over population sizes of *Corbicula* in their study area (the Altamaha River), largely because of the danger this posed to survival of endemic unionids in the drainage. Survival of such endemics may well depend on the availability of both undisturbed and low pH habitats (Mosquito Creek is an example of a low pH *disturbed* habitat, in which *Corbicula* densities can be high despite low individual fitness), from which recolonization could proceed once *Corbicula* populations have stabilized and environmental deterioration of such drainages is reversed.

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A NEW SPECIES OF *ENDODONTA* (PULMONATA, ENDODONTIDAE) FROM OAHU, HAWAII. – In the course of paleoecological investigations at Barbers Point, Oahu, an undescribed extinct species of *Endodonta* (a genus endemic to the Hawaiian Islands) was found to be a characteristic member of Recent and sub-Recent subfossil assemblages of nonmarine molluscs. Ecological disturbance, undoubtedly the result of activities of the prehistoric and modern human inhabitants of the Barbers Point region, has extirpated all but a few of the native land snail taxa formerly present. The findings of these paleoecological studies will be published elsewhere (Christensen & Kirch, in press; Kirch & Christensen, in prep.); the purpose of the present work is to provide a description of the previously unreported *Endodonta*.

Measurements and descriptive terminology are as defined by Solem (1976).

Endodonta kalaeloana new species. (Figs. 1-3). Adult shell 5.0-6.9 mm in diameter (range, mean and standard error of the mean of holotype [BPBM (Bernice P. Bishop Museum) 207190] and 41 paratypes from type locality [BPBM 207188, 207191-3] 5.0-6.5, 5.69 ± 0.061 mm), with $5\frac{1}{8}$-$6\frac{3}{8}$ whorls ($5\frac{1}{8}$-$6\frac{1}{8}$, 5.52 ± 0.040 whorls). Apex almost flat to slightly elevated, rate of whorl translation increasing to produce a spire slightly to moderately rounded in outline, last whorl rarely descending markedly at aperture. Height/diameter ratio 0.339-0.491 (0.339-0.444, 0.3816 ± 0.0033). Umbilicus widely open, diameter/umbilicus ratio 2.55-3.67 (2.55-3.33, 2.96 ± 0.026), U-shaped, the last 1-$1\frac{1}{2}$ whorls decoiling more rapidly (i.e., umbilical diameter increasing more rapidly). Apical whorls smooth or with low riblets. Postnuclear whorls with broad low protractive ribs (obsolete in later whorls; poorly developed throughout in some specimens) and numerous low spiral cords (more prominent below the periphery). Suture shallow, whorls weakly rounded above shallow supraperipheral sulcus; periphery sharply carinate; lower palatal wall flat below weak subperipheral sulcus, basal margin regularly rounded to obtusely angled margin of umbilicus; umbilical wall flat. Aperture inclined about 40° from shell axis. Parietal barriers two, extending posteriorly less than one-quarter whorl; upper parietal barrier high, twisted slightly upward, gradually descending anteriorly, expanded or bifid posteriorly; second parietal lower, bladelike or weakly expanded posteriorly; in a single specimen a trace located between the parietal barriers. Columellar barrier moderately high, bent upward from plane of coiling. Palatal barriers four (rarely five); three (in a single specimen four) below periphery, extending posteriorly less than one-eighth whorl, high, bladelike, subequal in size, slightly recessed; one (in a single specimen two, closely set) above periphery, moderately high, gradually descending anteriorly and extending almost to peristome; palatal traces usually three to four, less often two, rarely none, one or five (0-3 subperipheral, 0-3 supraperipheral in position), all located between third and fourth palatal barriers (in specimens having the usual four palatals).

FIGS. 1-3. *Endodonta kalaeloana* new species (not to scale). FIG. 1 (top). Apertural view, Paratype, BPBM 207191, shell diameter 6.5 mm. FIG. 2 (left). Apical view, Holotype, BPBM 207190, shell diameter 6.5 mm. FIG. 3 (right). Basal view, Paratype, BPBM 207192, shell diameter 6.1 mm.

Material[1]. Holotype: Hawaii, Oahu Island, Ewa District, ahupua'a (land division) of Honouliuli, Site 50-0a-B6-78 (sinkhole, distance ca 1.4 km, bearing 341° from Barbers Point Light) Sample 8 (Layer II, depth 20-30 cm below surface), BPBM 207190, shell height 2.5 mm, diameter 6.5 mm, whorls six. Paratypes: Hawaii, Oahu Island, Ewa District, ahupua'a of Honouliuli, Site B6-78 Sample 7 (Layer II, 10-20 cm), BPBM 207188-9 (18 measured adults, 119 other specimens); Sample 8, BPBM 207191-4 (23 measured adults, 212 other specimens); Site 50-80-12-2624 (large sinkhole, ca 1.1 km, bearing 343° from Barbers Point Light) Sample 3 (Layer II, 7-12 cm), BPBM 207203-4 (25 measured adults, 272 other specimens); Sample 4 (Layer II, 12-17 cm), BPBM 207205-6 (32 measured adults, 272 other specimens); Site 50-80-12-2712 (habitation feature, ca 0.9 km, bearing 005° from Barbers Point Light) Sample 3 (Layer I, 6-7/9 cm), BPBM 207209-10 (five measured adults, 14 other specimens); Ewa, coral plain below Sisal, C.M. Cooke, Jr., and C.N. Forbes, 16 February 1912, BPBM 35603 (17 measured adults, 13 other specimens); Ewa, coral plain below Sisal, in coral pits, C.M. Cooke, Jr., and C.N. Forbes, 16 February 1912, BPBM 35627 (eight measured adults, 17 other specimens). Ahupua'a of Puuloa, along Ewa Beach Road near telegraph [pole] 88, where cane stops, $\frac{1}{5}$ mile from sight [site?] of Puuloa Farms rental office, D.A. Welch, 7 September 1931, BPBM 105423 (10 measured adults, 14 other specimens). Additional material: additional specimens were recovered from other samples at Sites B6-78, 2624 and 2712, but were not used in the preparation of the above description.

Diagnosis. In shell morphology, *Endodonta kalaeloana* most closely resembles *E. laminata* (Pease 1866), a Kauai species that differs from it in having a more strongly and evenly elevated apex and spire, stronger and more numerous ribs, and a dissimilar arrangement of apertural trace barriers (in *E. laminata* accessory traces are often located between the columellar, first palatal, and second palatal barriers, and not more than two traces lie between the third and fourth palatals; *E. kalaeloana* lacks palatal traces except between the third and fourth palatal barriers, where three or more are found in most specimens). *E. binaria* (Pfeiffer 1856), another Kauai species, differs from the new species in having a more elevated spire, stronger sculpture and bifid palatal barriers. *E. apiculata* Ancey 1889, also of Kauai, has a sunken apex and much stronger sculpture (based upon specimens identified by C.M. Cooke, Jr.; none of Ancey's specimens of *E. apiculata* are held by Bishop Museum). The description of *E. rugata* (Pease, 1866), a poorly known species thought to inhabit Maui, cites the presence of a total of four columellar and palatal barriers; five, or rarely six, are found in *E. kalaeloana*. None of the four described Oahu species of *Endodonta* is likely to be confused with the new taxon: *E. ekahanuiensis* Solem 1976 is much smaller (shell diameter less than 3 mm), while *E. lamellosa* (Férussac 1824), *E. marsupialis* Pilsbry & Vanatta 1906, and *E. fricki* (Pfeiffer 1858) lack prominent shell sculpture.

Remarks. C.M. Cooke, Jr., recognized *Endodonta kalaeloana* as distinct from other members of the genus but did not prepare a description of it. The species undoubtedly is now extinct, but prior to human settlement of the Hawaiian Islands it apparently was abundant in the arid Ewa Plain of southwestern Oahu, a karstic region of emerged reef limestone extending from Kahe Point to Pearl Harbor. The species shows considerable variability in the number of accessory palatal traces present, but the major apertural barriers are virtually invariant (only two of 139 specimens had other than the typical complement of two parietal, one columellar and four palatal barriers). The mean values of such parameters as shell diameter and height/diameter ratio show some inter-sample differences (range of sample mean values 5.55-6.50 mm and 0.377-0.425, respectively), but not to a degree that would warrant taxonomic recognition. The name assigned to this species is from *Kalaeloa*, the Hawaiian name for Barbers Point.

Acknowledgements. The paleoecological studies that resulted in collection of the bulk of the material examined were conducted under contract to Archaeological Research Center Hawaii, Inc., for the U.S. Department of the Army, Corps of Engineers, Pacific Ocean Division. Scanning electron microscope photographs were prepared by Karen Margolis, Hawaii Institute of Geophysics, University of Hawaii.

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[1] Specimens collected by C.C. Christensen and P.V. Kirch, April 1980, unless otherwise stated. For descriptions of numbered archaeological sites, see Hammatt & Folk (1981): prefix (50-0a-, 50-80-12-) omitted from site designation after first mention in text.

BIO-ELECTRONIC TECHNIQUES FOR THE STUDY OF MOLLUSCAN ACTIVITY. – Bio-electronics offers effective techniques for obtaining information on movement and physiology of animals, and its use has grown significantly in recent years. Although electronic components are now small enough to be used on at least the larger mollusk species, none of the more than 1700 references of biotelemetric studies in the recent review of Ysenbrandt et al. (1976) concerns mollusks.

I recently conducted a study in the Philippines on the activity patterns of *Ryssota uranus* (Pfeiffer). This study was made in conjunction with research on the activity of *Varanus grayi* Boulenger, a large arboreal lizard. The snail's activity, home range, etc., were of particular interest to the *Varanus* study because the snails constitute a rather large portion of the lizard's diet. A discussion of the data obtained in the *Ryssota* study is being prepared for publication.

Techniques and discussion. During this study two techniques new to malacological research were employed. Both proved successful within the limitations discussed below. With modification, these limitations can be minimized and both techniques made highly valuable to future studies of molluscan behavior.

1. Biotelemetric transmitters. The transmitter used in this study was a simple blocking oscillator (see Shields, 1979) designed to operate in the FM entertainment band (Fig. 1). Battery size determined unit weight (5.5 g for transmitter and 7.5 g for battery in this study) and life expectancy. Maximum reception range was estimated at 100 m when used with a J.C. Penney Co., Inc., Model 1960 AM/FM receiver, but, within the limestone karst of the study area, reception distance was reduced to approximately 30 m.

I constructed the transmitters so that the components conformed in size and shape to the apex of the shell and so that the loop antenna laid in the suture (Fig. 1B). The completed transmitters were dipped in PDS Air Dry Plastic Coating (made by Plastic Dip International, St. Paul, Minnesota, U.S.A.) for waterproofing. The transmitters and battery pack were mounted on the shell with epoxy cement and sprayed with an acrylic paint for final waterproofing. It was found that snails cannot be kept in airtight containers (plastic bags, etc.) after transmitter mounting and prior to release due to the noxious fumes of many waterproofing agents.

Although data were obtained on activity patterns of *Ryssota uranus*, the technique had one major limitation: signal strength was so great that at close distances some directionality was lost, and only after a great deal of time and receiver detuning were the snails' exact positions located. As most snails do not move far during any one activity period, a signal transmitted over a wide area becomes a hindrance in determining the exact location of the snail. With modification of transmitter components, a weaker signal can be achieved whereby directionality is maintained at a maximum.

Precise location at close distances required detuning of the receiver. Detuning is accomplished by shortening the telescopic antenna usually provided on small FM receivers and/or tuning the receiver to pick up only the weakest signal possible when near the snail. Thus, the signal will be lost when the receiver is moved away from the transmitting snail. With practice, the snail can be found easily.

2. Light-emitting diodes (LED). The Radio Shack Model FRL-4403 flasher LED (made by Archer Electronic Parts; US$1.29 each) incorporates an electronic microchip in its base that causes the diode to switch on and off. The LED leads are attached to two 1.5V batteries connected in series (Fig. 2B). Battery size determines life of the unit (Duracell mercury button type No. TR 126 lasts approximately five days; silver oxide, and especially lithium types, would last much longer; smaller batteries, such as those used in hearing aids, last a proportionately shorter length of time). Assembly requires only the soldering of the leads (exhibiting polarity) to the appropriate battery terminals. While convenient to use, the flash rate is quite fast, thus shortening battery life.

A much longer-lived miniature flasher is shown in Fig. 2A. A detailed description of this flasher can be found in Wolcott (1977) and Kephart (1980). This flasher is slightly less convenient, because more components are used in its construction, making it larger. However, the size increase is offset by the fact that only one 1.5V battery is required (life expectancy is one month or more), so total weight increase is not great. These LEDs are available in several colors, sizes and shapes. Different capacitor values will provide a variety of flash rates (the flasher illustrated provides a flash rate of about 1/sec). Individual snails then can be identified from a distance by a combination of color and flash rates (the latter may be determined by recording the elapsed time for five or more flashes).

In both LED units, the polarity indicated (Fig. 2) for components must be maintained. Maximum light emission normally occurs at the distal tip of the LED, and this should be considered in mounting the unit to facilitate recognition from a distance. Maximum visual discrimination for the strongest LEDs is about 75 m.

In the present study, the unit shown in Fig. 2B was used. The LED unit was secured to the posterior portion of the upper surface of the body whorl with black electrician's tape (Fig. 2C), maximizing visibility from all angles while the snail was active. The tape was trimmed about the umbilicus and apertural lip to facilitate body movements. Reflective tape also was used in several places on the shell to increase the possibility of recapture in case of unit failure. The weight of the unit was 18 g, but this could be reduced substantially by the use of smaller batteries (with loss of unit life expectancy).

Because of the species' nocturnal habits, this technique proved highly successful in recording its activity. The snails were found easily and observed while active every night for the duration of the study. The snails became inactive when under a lighted headlamp, but were not distracted by the flashing LED.

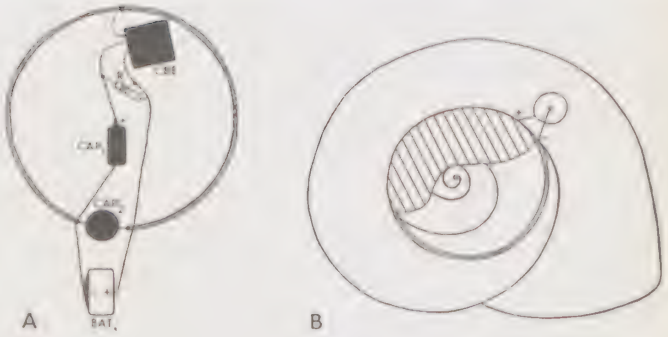

FIG. 1. Biotelemetric transmitters. **A**, Collector, base and emitter (CBE); resistor (R); electrolytic capacitor (CAP_1); ceramic disc capacitor (CAP_2); battery (BAT), one Duracell mercury button type. **B**, Mounting position on snail.

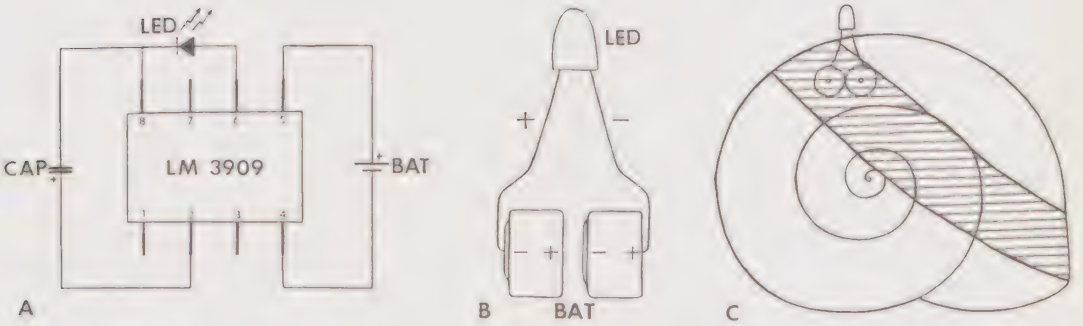

FIG. 2. Light-emitting diodes. **A**, Electrolytic capacitor (CAP); battery (BAT), Duracell 1.5V mercury button type; light-emitting diode (LED); integrated circuit (LM3909) (after Kephart, 1980). **B**, Light-emitting diode (LED), Radio Shack FRL-4403; batteries (BAT), two Duracell 1.5V mercury button type in series. **C**, Suggested mounting position on snail.

Although LEDs can be effective in the study of large nocturnal or arboreal snails, highly secretive species and juveniles of some species could impose limitations on their use. For example, a juvenile *Ryssota* with an attached LED promptly disappeared into deep cracks in the limestone, not usually inhabited by adults, rendering the LED useless. A radio transmitter would be more appropriate in such situations.

Another possible disadvantage is that the LED may attract predators, although this was not the case in the present study.

The transmitters and LEDs proved effective in determining home range, home site range, and daily activity patterns. Continued use and modification of these techniques are urged, for they are effective, easily constructed and operated, and inexpensive.

Acknowledgements. This study was made possible through a grant awarded by Sigma Xi, The Research Society, for the purchase of electronic components needed for both types of bio-electronic units. My thanks to Anne Tallent for the illustrations and to Fred G. Thompson, J.B. Burch, Walter Auffenberg and Rhoda Bryant for review of the manuscript.

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DISCUS ROTUNDATUS (MÜLLER) (GASTROPODA: PULMONATA) IN CALIFORNIA. – **Abstract.** The European and North African snail *Discus rotundatus* has been found in greenhouses and lathhouses in Santa Barbara, Ventura, Los Angeles and San Diego counties, California, U.S.A., in a warmer and more equable climate than introduced populations in eastern North America.

A sample of small snails collected by the California Department of Food and Agriculture at a nursery in Santa Barbara, California, U.S.A., and forwarded to me by R.D. Munkittrick, U.S. Department of Agriculture, proves to be *Discus rotundatus* (Müller 1774), a species native to Europe and North Africa (Fig. 1). The snails were collected January 8, 1981, in greenhouses and lathhouses on Orchid Drive, Santa Barbara. They were numerous under decaying wood on the ground and also were found under pots on the surface of the soil. The largest specimens in the sample are 5.7-6.1 mm in diameter with 6.25-6.50 whorls: as large or larger than usual in Europe (Kerney & Cameron, 1979). The smallest specimens are 2.4 mm in diameter with 3.5 whorls. *Zonitoides arboreus* (Say 1816) also was present but in lesser numbers. Voucher specimens of *D. rotundatus* are deposited in the Department of Invertebrate Zoology, California Academy of Sciences (catalog no. CAS 024666).

Dr. Tokuwo Kono has kindly informed me of three other occurrences of *Discus rotundatus* in California, from the records of the California Department of Food and Agriculture: (1) Camarillo, Ventura Co., with orchids in greenhouse, May 26, 1954; (2) San Gabriel, Los Angeles Co., on ground under benches in nursery, July 3, 1969; (3) Saticoy, Ventura Co., in greenhouses, April 11, 1978. The first two samples were identified by J.P.E. Morrison and W.J. Byas, respectively; the third, by Mr. Munkittrick, who also first identified the Santa Barbara infestation. One specimen from the Camarillo occurrence is in the U.S. National Museum of Natural History, Washington, D.C. (USNM 608348). It is 4.2 mm in diameter with 5.0 whorls. Specimens from San Gabriel and Saticoy were not detected in the USNM collection (J. Rosewater, pers. comm., Sept. 1981), but the search did turn up a single somewhat worn shell collected at Oceanside, San Diego Co., on fern, July 14, 1950, by H.H. Kiefer (California Department of Food and Agriculture) (USNM 595343). Whether the ferns were being grown under glass is not specified. The specimen is 4.65 mm in diameter with 5.0 whorls.

FIG. 1. *Discus rotundatus* (Müller), Santa Barbara, California, diameter 5.9 mm (CAS 024666).

In the Palearctic realm, *Discus rotundatus* has an extensive range from southern Scandinavia (south of 63°N; Evans, 1972) to Algeria (Pilsbry, 1948) and from Spain and Ireland on the west to the Ukraine on the east (Likhachev & Rammel'meier, 1952). Its span of altitude, to 2700 m in Switzerland (Kerney & Cameron, 1979), is one of the greatest for any European land mollusk (Godan, 1979). The preferred habitat is reported to be "moist sheltered places of all kinds: woods, under ground litter and stones, in damp herbage: often among rubbish in gardens" (Kerney & Cameron, 1979). In Britain and in the New World, the species is often abundant where found (Jacobson, 1954; Evans, 1972). It readily is spread by man and is known as an introduction in eastern North America from Massachusetts, New Jersey, New York and Newfoundland (Pilsbry, 1948; Jacobson, 1954; Dundee, 1974). Godan (1979) reported several accounts of its association with cultivated plants. At the present time, the California Department of Food and Agriculture does not regard it as an organism of economic importance. (However, like all non-native species of slugs and land snails [except *Helix aspersa* Müller 1774 and *Rumina decollata* (Linnaeus 1758) in eight southern California counties], to the California Department of Fish and Game it is a Prohibited Species and may not be imported into, transported within or possessed in the state [Calif. Fish and Game Commission, Title 14, Section 671].)

Discus rotundatus is well figured in color by Godan (1979: pl. 7, figs. 1, 2) and Kerney & Cameron (1979: pl. 3, figs. 7a-7c). The tightly coiled, delicately ribbed shell with bold reddish-brown axial striping scarcely could be confused with any other species now known from California.

The Californian occurrences reported here are all in the mild, Mediterranean climate of southern California, south of the Transverse Ranges. The fact that the Santa Barbara and possibly the San Gabriel and Oceanside occurrences are not in greenhouses indicates that *Discus rotundatus* can survive in this region outdoors, without direct temperature modification. It may, however, be restricted to areas receiving artificial irrigation. Given the very wide thermal tolerances evidenced by the species' native range, and its well-documented association with horticulture, it is somewhat surprising not to find *D. rotundatus* more widespread as an introduction, particularly in the colder, moister parts of the state. The thermal regime in its eastern North American range includes both a lower mean annual temperature and a much greater annual temperature range – about 20-25°C, compared to about 7-12°C for a strip running from Santa Barbara to San Gabriel (data from Elford, 1970; Wolfe, 1979). It is possible that European *D. rotundatus* may include physiological races with differing thermal tolerances. If, for instance, the eastern introductions had a northern European source and the California introductions a southern source, their ultimate thermal zones of inhabitancy could be quite different.

Acknowledgments. I am indebted to R.D. Munkittrick (U.S. Department of Agriculture) for calling to my attention the Santa Barbara occurrence and to T. Kono (California Department of Food and Agriculture) for furnishing additional records. Joseph Rosewater (U.S. National Museum of Natural History) and J.H. McLean (Los Angeles County Museum of Natural History) searched the collections under their care for pertinent material. Larry L. Eng (California Department of Fish and Game) read the manuscript and advised on the legal implications.

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TAXONOMIC AND NOMENCLATURAL CHANGES SINCE 1960 IN SNAILS AND SLUGS OF QUARANTINE SIGNIFICANCE TO THE UNITED STATES. – In 1959, I was commissioned by the U.S. Department of Agriculture to write a snail identification guide for use by animal and plant quarantine inspectors at the various ports of entry into the United States. This manual was published in 1960 as *Some snails and slugs of quarantine significance to the United States*. Later, the manual was reprinted (in revised format) in *Sterkiana* at the request of the editor, Aurèle LaRocque, and the original version was reprinted in 1967 by the Naval Medical Field Research Laboratory, Camp Lejeune, North Carolina. The manual is still widely used in the United States and elsewhere, and permission has just been granted to have the original manual reproduced in Australia for use by quarantine officials and others in that country.

In the 23 years since the guide was written, the increase in knowledge about land and freshwater mollusks has necessitated various taxonomic and nomenclatural changes in some of the taxa dealt with in the manual. Because of the continued wide use of the manual, it seems desirable to record these changes. That is the purpose of this brief article.

If one uses chronological priority in assigning familial names (a practice which, incidentally, is not universally accepted by zoologists), then several well-known family names will be replaced with older names. These are as follows: Zonitidae Mörch 1864 = Vitrinidae Fitzinger 1833; Bulimulidae Tryon 1867 = Orthalicidae Albers-Martens 1860; Bradybaenidae Pilsbry 1934 (Fruticicolidae Lindholm 1927) = Xanthonychidae Strebel & Pfeffer 1879; Helicellidae Wenz 1923 = Hygromiidae Tryon 1866.

Snails of the land pulmonate suborder Sigmurethra are now divided into three divisions (infraorders), rather than two (Baker, 1962). The sigmurethran snails mentioned in Burch (1960) are now classified as follows.

Infraorder **Holopodopes** H.B. Baker 1962
- Family Achatinidae Swainson 1840
  - Genus *Achatina* Lamarck 1799
  - Genus *Cecilioides* Férussac 1814
  - Genus *Lamellaxis* Strebel & Pfeffer (in Strebel) 1882
  - Genus *Opeas* Albers 1850
  - Genus *Rumina* Risso 1826
  - Genus *Subulina* Beck 1837
- Family Orthalicidae Albers-Martens 1860 (Bulimulidae Tryon 1867)
  - Genus *Porphyrobaphe* Shuttleworth 1856
- Family Spiraxidae Gray 1860
  - Genus *Euglandina* Fischer & Crosse 1870 (see Baker, 1963; *Euglandina* was placed previously in the Oleacinidae (see Pilsbry, 1946))

Infraorder **Aulacopoda** Pilsbry 1896
- Family Arionidae Gray (in Turton) 1840
  - Genus *Arion* Férussac 1819
- Family Limacidae Rafinesque 1815
  - Genus *Deroceras* Rafinesque 1820
  - Genus *Limax* Linnaeus 1758
  - Genus *Milax* Gray 1855
- Family Testacellidae Gray (in Turton) 1840
  - Genus *Testacella* Draparnaud 1801
- Family Vitrinidae Fitzinger 1833 (Zonitidae Mörch 1864)
  - Genus *Oxychilus* Fitzinger 1833

Infraorder **Holopoda** Pilsbry 1896
- Family Camaenidae Pilsbry 1895
  - Genus *Solaropsis* Beck 1837
- Family Helicidae Rafinesque 1815
  - Genus *Cepaea* Held 1837
  - Genus *Helicigona* Risso 1826
  - Genus *Helix* Linnaeus 1758
  - Genus *Otala* Schumacher 1817
  - Genus *Theba* Risso 1826
- Family Hygromiidae Tryon 1866 (Helicellidae Wenz 1923)
  - Genus *Cochlicella* Risso 1826
  - Genus *Helicella* Férussac 1821
  - Genus *Hygromia* Risso 1826
  - Genus *Monacha* Fitzinger 1833
- Family Xanthonychidae Strebel & Pfeffer 1879 (Bradybaenidae Pilsbry 1934; Fruticicolidae Lindholm 1927)
  - Genus *Bradybaena* Beck 1837

The Hydrobiidae Troschel 1857 are now conceded by many taxonomists (but by no means all) to be distinct at the family level from the Bithyniidae Gray 1857. Further, the Pomatiopsinae Stimpson 1865, which historically have fluctuated in recognition between subfamily and full family, have been considered most recently to be a distinct family (Davis, 1979). Following such a scheme, the intermediate hosts of schistosomiasis japonicum in the Far East would be placed under the familial name Pomatiopsidae and in the genus *Oncomelania* Gredler 1881 (generically distinct from *Pomatiopsis* Tryon 1862; e.g., see Davis, 1967). *Katayama* Robson 1915 is a synonym of *Oncomelania* Gredler 1881. At the level of the lower taxonomic categories, the snails carrying *Schistosoma japonicum* Katsurada all belong to one species (e.g., see Burch, 1964), but with several geographical races distinguished. Thus, the classification for these snails generally in use now is as follows (see Burch, 1967; Davis, 1979; et al.).

Oncomelania hupensis hupensis Gredler 1881, China mainland
O. hupensis nosophora (Robson 1915), Japan
O. hupensis formosana (Pilsbry & Hirase 1906), Taiwan
O. hupensis chiui (Habe & Miyazaki 1962), Taiwan
O. hupensis quadrasi (Moellendorff 1895), Philippines
O. hupensis lindoensis Davis & Carney 1973, Sulawesi

The lymnaeid *Fossaria ollula* (Gould 1859) has been placed most recently in the genus *Austropeplea* Cotton 1942, largely because of its chromosome number (Inaba, 1969). It may be identical with "*Lymnaea viridis*" Quoy & Gaimard 1833 of Guam.

In the Planorbidae, *Armigerus obstructus* (Morelet) and *Planorbina glabrata* (Say) are now placed in the genus *Biomphalaria* (e.g., see Malek, 1969). Opinion 735 of the International Commission on Zoological Nomenclature (1965) has over-ruled the earlier names *Planorbina* Haldeman 1842, *Taphius* H. & A. Adams 1855 and *Armigerus* Clessin 1884 in favor of *Biomphalaria* Preston 1910.

Physopsis Krauss 1848 is now generally conceded to be a subgenus of *Bulinus* Müller 1781.

The class Amphineura von Ihering 1876, as a composite group containing chitons and solenogasters, is no longer recognized as a monophyletic taxon, but instead is divided into two classes, the Polyplacophora de Blainville 1816 (chitons) and Aplacophora von Ihering 1876 (solenogasters) (Scheltema, 1978).

The bivalves have commonly gone under the class name Pelecypoda Goldfuss 1820, and also under Lamellibranchia de Blainville 1824, but currently the older name Bivalvia Linnaeus 1758 is coming into more general usage.

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ABSTRACTS OF PAPERS

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A MINISYMPOSIUM AND WORKSHOP

ECOLOGICAL EFFECTS AND BIOGEOGRAPHY OF AN INTRODUCED MARINE SPECIES: THE PERIWINKLE, *LITTORINA LITTOREA*

(A zoological, botanical and ecological symposium)

Conveners

James T. Carlton
Woods Hole Oceanographic Institution

Donald P. Cheney
Northeastern University

Geerat J. Vermeij
University of Maryland

ABSTRACTS OF PAPERS

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PREDATION ON THE PERIWINKLE *LITTORINA LITTOREA* BY NORTHWESTERN ATLANTIC CRABS AND LOBSTERS

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Abstract

Predation on the periwinkle, *Littorina littorea* (Linnaeus), by the green crab, *Carcinus maenas* (Linnaeus), rock crab, *Cancer irroratus* (Say), jonah crab, *Cancer borealis* (Stimpson), and American lobster, *Homarus americanus* (Milne-Edwards), was observed in the laboratory.

Subtidal periwinkles were collected from the Bay of Fundy at St. Andrews, New Brunswick, and sorted into three size classes based on shell height (10-15 mm, 16-20 mm and 21-28 mm). Each predator was given five periwinkles per size class per day. The male lobster (94 mm carapace length, CL) and largest of three male jonah crabs (119 mm, 120 mm and 135 mm carapace width, CW) were successful in crushing periwinkles up to 28 mm in height. Predation by three male green crabs (72 mm, 75 mm and 76 mm CW) and three male rock crabs (88 mm, 106 mm and 125 mm CW) was limited to prey sizes less than 20.0 mm.

Over 15 days, the largest jonah crab exhibited the highest mean daily predation rate of all the decapods observed, 3.93 + 0.74 S.E. periwinkles day^{-1}, followed by a green crab (76 mm CW), 3.07 + 0.65 S.E. periwinkles day^{-1}, rock crab (88 mm CW), 1.64 + 0.27 S.E. periwinkles day^{-1} and lobster (94 mm), 0.71 + 0.21 S.E. periwinkles day^{-1}. The number of different feeding strategies utilized by a predator was inversely related to the number of periwinkle size categories fed upon. Green crabs preferred the smallest periwinkle size class, but exhibited the greatest number of shell-breaking techniques. The jonah crabs and lobster fed on all prey size classes but employed only two feeding methods; both methods involved a pressure applied to one location (usually the body whorl) over a period of 1 to 1.5 min. Rock crabs fed on all size classes but showed a preference for the mid size category, using three shell-breaking techniques.

We hypothesize that the foraging strategies exhibited by the predators are related to: 1) the rate at which predators encounter prey, and 2) predator-prey size relationship.

GEOGRAPHIC VARIATION IN *PAGURUS LONGICARPUS*: IS *LITTORINA LITTOREA* A CAUSAL AGENT?

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Abstract

The shallow water hermit crab *Pagurus longicarpus* Say exhibits geographic variation along the eastern coast of North America. Three localities – Beaufort, North Carolina; Barnegat Bay, New Jersey; Guilford, Connecticut – display representative variation of hermit crab morphology, sexual dimorphism and population structure.

Guilford males are larger and have relatively smaller chelipeds and periopods than Beaufort males. Guilford females are smaller and have relatively smaller chelipeds than Beaufort females. Hence, sexual dimorphism is extreme at Guilford and slight at Beaufort. In the Beaufort intertidal, sex ratio as a function of size (which may be indicative of population structure) shows a pattern commonly seen in crustaceans. In the Guilford intertidal, the pattern is peculiar.

The introduction of *Littorina littorea* (Linnaeus) greatly increased the number of large shells available to and utilized by *Pagurus longicarpus* at Guilford and other New England localities. While the large size of Guilford males may be due to the effects of *L. littorea* shells (c.f., Drapkin, 1963, *Dokl. Akad. Nauk SSSR*, biol. sci., 151: 700-703 [English transl., 1964, 151: 964-966]), this hypothesis cannot easily explain data from Barnegat Bay. Here *P. longicarpus* are similar to those from Guilford despite the scarcity of *L. littorea* shells. Finally, it is of note that evolutionary trends which parallel those seen in *P. longicarpus* ("lithodization") occur in some other hermit crab species at northern latitudes.

THE CURRENT STATUS OF THE 100-YEAR WAR BETWEEN NATIVE "MUD" SNAILS, *ILYANASSA OBSOLETA*, AND A DOMINANT COMPETITOR AND PREDATOR, THE EUROPEAN PERIWINKLE, *LITTORINA LITTOREA*

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Marine Biological Laboratory, Woods Hole, Massachusetts 02543, U.S.A.

Abstract

Interactions ranging from competition for space to predation between native "mud" snails, *Ilyanassa obsoleta* (Say), and the European periwinkle, *Littorina littorea* (Linnaeus), have been studied for two summers (1980-81) in Barnstable Harbor, Massachusetts. Evidence for both kinds of interactions are striking, and support Dimon's (1905, The mud snail, *Nassa obsoleta*. *Cold Spring Harbor Monogr.*, (5): 48 pp) original prediction that the exotics were slowly displacing the native. *I. obsoleta* require "solid" substrates to attach egg capsules (e.g., tube-caps of *Diopatra cuprea* (Bosc), *Zostera*, wood, peat of marsh banks, *Spartina*, and algae such as *Codium*, another exotic species), yet all these substrates are densely populated by *L. littorea*. *L. littorea* will ingest eggs deposited on all of these surfaces in the laboratory. Rarely are entire capsules consumed. On rare occasions the capsules are defecated intact and the larvae emerge. *I. obsoleta* has developed an avoidance of *L. littorea*, although laboratory studies have failed to detect any chemoreceptory responses. *I. obsoleta* delays the deposition of egg capsules, and subsequently lays fewer capsules, when *L. littorea* is present than when not. *L. littorea*, added to tide pools, causes *I. obsoleta* to disperse and lay few egg capsules; when removed from tide pools or the edge of the marsh, *I. obsoleta* expands its distribution. Experiments currently in progress will establish whether *L. littorea* has forced *I. obsoleta* into "sub-optimal" habitats (growth experiments) or has altered its migratory patterns (marked snails). Changes in the distribution and abundance of *L. littorea* on the sand flats will also be discussed.

THE HISTORICAL BIOGEOGRAPHY OF *LITTORINA LITTOREA* ON THE ATLANTIC COAST OF NORTH AMERICA, AND IMPLICATIONS FOR THE INTERPRETATION OF THE STRUCTURE OF NEW ENGLAND INTERTIDAL COMMUNITIES

James T. Carlton

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Abstract

Despite very rare subfossil and possibly fossil occurrences of *Littorina littorea* (Linnaeus) in eastern Canada, the first living specimens of this periwinkle were not found in North America until 1840 in the Gulf of St. Lawrence, at Pictour. The simplest explanation of the data is that the modern populations are the result of intentional introductions by European settlers in the early 19th century, and that earlier occurrences represent populations of *L. littorea* that lived in Canada until the end of the 13th century. Sequential discoveries included Halifax (1854), the Bay of Fundy (1861-1862), Portland, Maine (1870), the north shore of Cape Cod (1870-1872), Woods Hole (1875), Long Island Sound (1879-1881) and Atlantic City, New Jersey (1888), a southward extension of range climaxed by its appearance in 1890 at Cape May, New Jersey. In the 20th century, *Littorina* made localized appearances on isolated rock jetties on the "Delmarva" (Delaware, Maryland, and Virginia) Peninsula, between the mouths of Delaware Bay and Chesapeake Bay. Thus, within a span of 20 years (1861-1881), *L. littorea* became the dominant intertidal herbivore in many areas between Canada and New York.

The establishment of a colonizing species in ecological time as both an aspect dominant and a structural dominant in natural communities permits the consideration of a number of testable hypotheses concerning the nature and extent of community reorganization, with emphasis on predicted internal patterns of organization of a community whose structure in part is not the result of evolutionary processes. A model is proposed which synthesizes demonstrated, implied or suggested roles of *Littorina littorea* in regulating community structure, and which identifies yet uninvestigated, or only partially investigated, habitats in which *Littorina* may be exerting an important regulatory influence on both floral and faunal community components. As an example of the secondary and tertiary effects of the introduction of *L. littorea*, the nature of the reliance on *Littorina* shells by native hermit crabs (*Pagurus longicarpus* Say and *P. acadianus* Benedict) both north and south of Cape Cod is explored.

THE ROLE OF *LITTORINA LITTOREA* GRAZING ON RECRUITMENT AND DISTRIBUTION OF ALGAE IN THE LOWER INTERTIDAL ZONE

Donald Cheney

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Abstract

Littorina littorea (Linnaeus) clearly plays a dominant role in determining the composition, abundance and diversity of algae in the lower intertidal zone of New England. Grazing experiments have been conducted in the laboratory and field on several of the most common ephemeral algae and the two dominant perennial algae, *Chondrus crispus* Stackhouse and *Fucus distichus* Linnaeus. The effect of grazing on recruitment in the latter was assessed by determining the susceptibility of juveniles of various ages to *L. littorea* grazing. Results indicate that grazing pressure (= snail density) plays a key role in determining the composition and abundance of green ephemerals, as well as in determining which perennial alga will dominate. This study provides new evidence that *F. distichus*, which can grow at five times the rate of *Chondrus*, is the competitive dominant, and that the abundance of *Chondrus* is dependent upon grazing pressure. The principal reason for these species' distribution differences is that *Chondrus* juveniles exhibit anatomical adaptations to grazing which are lacking in *Fucus*. Further, *Fucus* was found to be preferred over *Chondrus* for all ages tested. Based upon these findings, a simple model will be proposed relating exposure, snail density and perennial algal composition. Preliminary field data so far support predictions of the model.

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SEASONAL AND ANNUAL VARIATIONS IN ABUNDANCE OF *LITTORINA LITTOREA* AT CAPE ANN, MASSACHUSETTS, 1935-37 AND 1956-58

Ralph W. Dexter

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Abstract

The marine communities at Cape Ann, Massachusetts, were studied in the summers of 1933-37 and 1956-60 along the Annisquam tidal inlet from Gloucester Harbor to Ipswich Bay. From intertidal quadrat samplings (¼ sq m) made in 1935-37 and 1956-58 on rocky shores, high and low salt marshes and a mussel bed, the populations of *Littorina littorea* (Linnaeus) are analyzed seasonally and annually.

Differences in mean population size within a single season were considerable (0-170). Rocky shores were nearly equally divided between increased and decreased populations. High marshes predominantly lost, and low marshes predominantly gained in population size. The mussel bed predominantly lost during the same season. The level of peak abundance of vertical distribution in a single season (including 1960 data) was as follows: half of the samples (14) remained the same; one quarter (eight) shifted upward, and one quarter (seven) shifted downward.

Annual changes of mean population also varied considerably (1-215). Rocky shores were equally divided between those gaining and losing both in the 1930's and the 1950's. High marshes mostly gained in the 1930's, but were equally divided in the 1950's. Low marshes were equally divided in the 1930's, but predominantly gained in the 1950's. The mussel bed declined in abundance both in the 1930's and the 1950's.

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NEW ENGLAND TIDE POOL COMMUNITIES: FIELD STUDIES, MODELS AND PREDICTIONS

Judith Pederson and Charles Puccia

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Abstract

We are using field data to test how well loop analysis models and qualitative methods can predict New England tide pool community patterns. Based on our own observations and on findings cited in the literature, we have identified six important variables: (1) adult *Littorina littorea* (Linnaeus), (2) juvenile *L. littorea*, (3) *Chondrus crispus* Stackhouse, (4) ephemeral algae, (5) microflora, and (6) *Carcinus maenas* (Linnaeus). From interactions of these variables, we have developed eight alternative loop models. Because there are divergent observations and hypotheses concerning community structure, inconsistent predictions between models emerge suggesting these are important links in the system. We are focusing our field studies on some of these inconsistent predictions.

Although the work is still in progress, we have data suggesting that one of the underlying assumptions is not documented in our study. Lubchenco (1978, *Am. Nat.*, 112: 23-39) suggested that in tide pools ephemeral algae outcompete *Chondrus* in the absence of *Littorina littorea* but *Chondrus* outcompetes ephemerals in the presence of the snails. Our findings indicate that in the presence of snails (500-1100/m^2) both *Chondrus* and ephemeral algal cover are lower relative to tide pools with fewer snails (10-50/m^2). Thus, there is a positive correlation between *Chondrus* and ephemeral algal cover. These and other preliminary findings will be discussed.

ECOLOGICAL ASPECTS OF HOST PARASITE INTERACTIONS IN MARINE SNAILS WITH SPECIAL REFERENCE TO THE GENUS *LITTORINA*

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Abstract

Marine gastropods are parasitized by a wide variety of organisms representing numerous taxa, the most common being the digenetic trematodes. While gastropods are most frequently the first intermediate hosts for digenes, they occasionally are second intermediate hosts, and rarely final hosts.

Trematodes have a variable but significant effect on their gastropod hosts. The type of pathology produced and its intensity are dependent on the degree of infection as well as the species of parasite involved. Destruction of the digestive gland, sex reversal, castration, behavioral modifications, and mortalities due to reduced physiological tolerances are common (Wright, 1966, *Helminthol. Abstr.*, 35: 207-224; Lauckner, 1980, Diseases of Mollusca: Gastropoda. *In: Disease of marine animals*, vol. 1, pp. 311-424). The consequences of these pathologies and parasitism in general have been overlooked in the overwhelming majority of ecological and physiological studies of marine gastropods. This is a serious oversight considering that parasitism in the intertidal zone is a fairly common occurrence. There have been reports of incidences as high as 75.5% in populations of *Littorina saxatilis* (Olivi) (Pohley, 1976, *Mar. Biol.*, 37: 179-186).

The physical and biological factors influencing patterns of geographical distribution and intertidal zonation of rocky shore gastropods have been extensively studied and amply documented. However, similar studies of the trematode parasites are noticeably absent from the literature. The most extensive studies have been conducted in Britain by James (1968, *J. nat. Hist.*, 2: 329-343; 1971, *4th Europ. mar. Biol. Symp.*, pp. 179-196), who examined the trematodes of a number of gastropod species but concentrated on littorines. His conclusions were based on the fact that the life cycles of trematodes can be divided into three major groups with differences in host and ecological specificity. Those with two free living stages were found on the lower shores of more sheltered coasts, while those lacking free living stages were associated with the littoral fringes of exposed areas. Cycles having just one free living stage had a wider distribution pattern. Though his study was not geographically extensive, his observations that parasite distributions are in large measure due to the relative abundance of final hosts in a given locale seems to hold true for other coasts.

GRAZING PATTERNS OF THE PERIWINKLE

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Abstract

Two abundant, sessile organisms, the green alga *Enteromorpha* and the barnacle *Balanus balanoides* (Linnaeus), are strongly affected by *Littorina littorea* (Linnaeus). At very low densities, *Littorina* can maintain initially bare areas clear of *Enteromorpha* while higher densities are required to eliminate established patches. With increasing *Littorina* densities, *Balanus* abundance first increases and then decreases. At low periwinkle densities *Enteromorpha* interferes with *Balanus* settlement, but at moderate snail densities the alga is removed and barnacle settlement improves. Newly settled barnacle cyprids appear to be dislodged at high periwinkle densities.

Experimental manipulation of periwinkle behavior through the use of partial cages shows that *Enteromorpha* can persist due to an interaction between snail behavior and surface irregularities. Certain areas are consistently missed which would normally be reached by a randomly moving grazer. There is no such refuge for *Balanus*. These results suggest that behavior-mediated effects may play a role in maintaining diversity in the rocky intertidal.

GRAZER-INDUCED DISTRIBUTIONAL PATTERNS OF INTERTIDAL ALGAE IN MAINE

Robert L. Vadas

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Abstract

Algal colonization and development in Maine is primarily a seasonal event (December to May). Vertical feeding migrations and feeding aggregations by *Littorina littorea* (Linnaeus) greatly modify patterns established through settlement behavior, physiological tolerances, competition or other processes. Visual observations, denuded plots and grazer exclusion cages were used to study the impact of *L. littorea* on vegetation patterns. Late winter or early spring grazing excursions produced distinct bands (zones) of algae. Feeding aggregations in the lower intertidal produced dynamic mosaic patterns on these shores.

GROWTH INHIBITION OF THE NATIVE *LITTORINA SAXATILIS* BY INTRODUCED *LITTORINA LITTOREA*

Sylvia Behrens Yamada and Randa Ali Mansour

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Wellesley, Massachusetts 02181, U.S.A.

and

Marine Biological Laboratory, Woods Hole, Massachusetts 02543, U.S.A.

Abstract

Since its introduction to North America, *Littorina littorea* (Linnaeus) has become the most abundant periwinkle in the low and mid-intertidal zone on both sheltered and exposed coasts. The possible effect of this introduction on native populations of *L. saxatilis* (Olivi) was investigated in two experiments on the south side of Cape Cod, Massachusetts.

In the pilot experiment, 18 cages were placed on pilings located near Nobska Point, Cape Cod, at high and low tide levels for 17 days. The growth rate of individuals (measured as lip increments) and the relative food abundance in each cage were determined. Both species grew significantly more in the mid-intertidal zone than in the supra-tidal zone. Intraspecific competition for food limited the growth of *Littorina littorea* in the supra-tidal zone. At the mid-intertidal zone, *L. littorea* depressed the growth of *L. saxatilis*.

These results led to an experiment in which 40 cages were placed at high and low tide levels on Gansett Beach, Cape Cod, for 19 days. Both species grew more in the mid-intertidal zone than in the supra-tidal zone. At the mid-intertidal zone, *Littorina littorea* depressed the growth of *L. saxatilis*. Intraspecific competition for food no longer appeared to limit the growth of *L. littorea*. The results of both experiments indicate that in the absence of *L. littorea*, *L. saxatilis* would have a broader vertical range.

ASSOCIATION OF *LITTORINA OBTUSATA* AND FUCOID ALGAE: EFFECTS OF COMPETITION WITH *LITTORINA LITTOREA*

Robin Hadlock Seeley

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Abstract

Association of *Littorina obtusata* (Linnaeus) with the brown fucoid seaweeds (*Fucus* spp., *Ascophyllum nodosum* (Linnaeus)) has long been observed on eastern and western Atlantic shores. The goal of my studies has been 1) to determine the precise pattern of association between *L. obtusata* and fucoids, and 2) to identify selective factors (feeding specialization, predation, competition) maintaining the association.

Field surveys (1978-1981) have revealed that *Littorina obtusata* becomes less restricted to fucoid algae as one moves from high to lower intertidal zones. In the high fucoid zone, *L. obtusata* lives almost exclusively on *Ascophyllum nodosum*. In the low fucoid zone, *L. obtusata* is abundant on *Fucus* but shares the red algal understory with *L. littorea* (Linnaeus). In the lowest (red algal) zone, where fucoids are rare, both *L. obtusata* and *L. littorea* are found primarily on *Chondrus crispus* Stackhouse.

Early results of controlled diet experiments (in progress) indicate that *Littorina obtusata* grows well when restricted to feeding on *Fucus* or *Ascophyllum*, while *L. littorea* grows poorly on this diet. Both periwinkles grow quickly on a diet of *Ulva lactuca* Linnaeus. Fewer individuals of *L. obtusata* are crushed or drilled on fucoid substrata than on non-fucoid (rock or understory) substrata. Finally, the presence of *L. littorea* has no significant effect on mortality, growth or habitat selection of *L. obtusata*.

In conclusion, although past competition with *Littorina littorea* may have selected for the "preference" of *L. obtusata* for a fucoid algae microhabitat, this periwinkle/algae association appears to be currently maintained by 1) crab and *Thais* predation on non-fucoid substrata, and 2) the unusual ability of *L. obtusata* to feed and grow on fucoid algae.

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RESPONSE OF *LITTORINA LITTOREA* TO THE COMING OF THE GREEN CRAB IN NORTH AMERICA

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Abstract

The green crab *Carcinus maenas* (Linnaeus), which co-occurs with its prey *Littorina littorea* (Linnaeus) in Europe, began to spread north of Cape Cod in the early twentieth century and reached Halifax in 1954. Populations of *L. littorea* north of Cape Cod lived in the absence of the green crab for 40 to 100 years. Frequencies of predator-induced shell repair in *L. littorea* rose after the arrival of *C. maenas*, but *L. littorea* did not respond adaptively by increasing its shell thickness. In other parts of its range, *L. littorea* showed no temporal variation in either frequency of repair or shell thickness, except in Denmark, where both declined after 1930. Dispersal and developmental limitations may account for the lack of adaptive response to a change in the selective environment which was perceived by *L. littorea* in North America.

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NEWS AND ANNOUNCEMENTS

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MALACOLOGY COURSE IN THE PHILIPPINES, 1981. – On 13 July-5 August 1981, the Second National Training Course on Medical Malacology was given in the Philippines (Manila and Sorsogon). It was organized by Dr. J.B. Burch, The University of Michigan, Ann Arbor, Michigan, U.S.A. Lecturers, besides Dr. Burch, included Dr. B.C. Dazo, World Health Organization, Western Pacific Region (WHO Operational Officer for the Course); Dr. Caridad Ancheta, Dr. Benjamin Cabrera, Dr. Edito G. Garcia, Prof. Nonette L. Jueco, Institute of Public Health, University of the Philippines; Dr. Gloria Enriquez, Dr. Ronaldo Garcia, Dr. Ruben Umaly, Department of Zoology, University of the Philippines;Dr. Roque Burio, Dr. Julian Noseñas and Mr. Manuel Santos, Schistosomiasis Control and Research Service, Ministry of Health, Manila; and Mr. Angel Bautista and Mr. Jaime Cabrera, National Museum, Manila. The course was sponsored by the Schistosomiasis Research and Control Service, Ministry of Health, Manila, and supported by the World Health Organization, Regional Office for the Western Pacific, Manila, Philippines. The course comprised lectures, laboratory practical exercises and field trips, and covered various aspects of molluscan biology, including classification, geological history, zoogeography, evolution, anatomy, physiology (respiration, feeding and digestion, excretion and endocrinology), reproduction, genetics, cytogenetics and cytotaxonomy, medical malacology (snails and trematodes of medical importance, epidemiology of snail-mediated diseases, chemotherapy, and snail surveillance and control), laboratory and field methods, and research methodology.

LITTORINA MINISYMPOSIUM AND WORKSHOP. – The First North American Symposium on *Littorina*, "Ecological effects and biogeography of an introduced marine species: the periwinkle, *Littorina littorea*", a zoological, botanical and ecological symposium, was held on 28-30 August 1981 at the Marine Science Institute, Northeastern University, Nahant, Massachusetts. The Conveners of the Symposium were Dr. James T. Carlton (Woods Hole Oceanographic Institution), Dr. Donald P. Cheney (Northeastern University) and Dr. Geerat Vermeij (University of Maryland). The program is given below. The abstracts of the papers are on p 143-150.

PROGRAM

Session 1

Donald Cheney. Introduction and raison d'etre.

James Carlton. The historical biogeography of *Littorina littorea* on the Atlantic coast of North America, and implications for the interpretation of the structure of New England intertidal communities.

Michael Beattie and Robert Elner. Predation on the periwinkle *Littorina littorea* by Northwestern Atlantic crabs and lobsters.

Neil Blackstone. Geographic variation in *Pagurus longicarpus*: is *Littorina littorea* a causal agent?

Gayle Brenchley. The current status of the 100-year war between native "mud" snails, *Ilyanassa obsoleta*, and a dominant competitor and predator, the European periwinkle *Littorina littorea*.

Session 2

Donald Cheney. The role of *Littorina littorea* grazing on recruitment and distribution of algae in the lower intertidal zone.

Ralph Dexter. Seasonal and annual variations in abundance of *Littorina littorea* at Cape Ann, Massachusetts, 1935-37 and 1956-58.

Judith Pederson. New England tide pool communities: field studies, models, and predictions.

Peter Petraitis. Grazing patterns of the periwinkle.

Jeffrey Pondick. Ecological aspects of host-parasite interactions in marine snails, with special reference to the genus *Littorina*.

Robin Hadlock Seeley. Association of *Littorina obtusata* and fucoid algae: effects of competition with *Littorina littorea*.

Field trip: protected and exposed intertidal sites at Nahant.

Session 3

Robert Vadas. Grazer induced distributional patterns of intertidal algae in Maine.

Geerat Vermeij. Response of *Littorina littorea* to the coming of the green crab in North America.

Sylvia Behrens Yamada and Randa Mansour. Growth inhibition of the native *Littorina saxatilis* by introduced *Littorina littorea*.

James Carlton. Rocky intertidal (herbivore) ecology of Scotland, Iceland, and New England: a comparative slide show study.

Group discussion (questions, problems, and directions); short subjects and slide presentations.

Geerat Vermeij. Some littoral conclusions.

MEETING OF THE SOCIETY FOR EXPERIMENTAL AND DESCRIPTIVE MALACOLOGY. – The 1982 annual business meeting of the Society for Experimental and Descriptive Malacology was held on 6 February 1982 in Ann Arbor, Michigan, U.S.A.

SUMMER 1982 MALACOLOGY COURSE AT THE UNIVERSITY OF MICHIGAN. – The Division of Biological Sciences of The University of Michigan will offer a course in "Biology of Mollusks" (Zoology 438) during the 1982 summer half-term (July to mid-August). This course will be open to both undergraduate and graduate students. For information regarding registration, write to Admissions Office, 1220 Student Activities Building, The University of Michigan, Ann Arbor, Michigan 48109. For information on course content, write to Dr. J.B. Burch, Department of Ecology and Evolutionary Biology, Division of Biological Sciences, The University of Michigan, P.O. Box 2749, Ann Arbor, Michigan 48106, U.S.A.

UNITAS MALACOLOGICA. – *Unitas Malacologica* is an international organization of malacologists and malacological societies whose goal is to support malacological research throughout the world and to regularly organize international malacological Congresses. The originally European society, founded in 1962 in London, was changed into a more broadly international organization in 1977 and now has more than 200 members all over the world. Its legal domicile is Basle, Switzerland. The annual subscription is 20 Swiss francs. This membership fee includes the Proceedings of the Congresses, held every third year. The last Congress was held in Perpignan, France, in 1980. The next International Malacological Congress will be held in Budapest, Hungary, in 1983.

Questions and applications with respect to membership should be sent to the Secretary, Dr. Oliver E. Paget, Natural History Museum, Burgring 7, A-1014, Vienna, Austria.

THE EIGHTH INTERNATIONAL MALACOLOGICAL CONGRESS, sponsored by the *Unitas Malacologica*, will be held in Budapest, Hungary, from 29 August to 3 September 1983. Further information can be obtained by writing to Dr. László Pintér, *Unitas Malacologica*, c/o Natural History Museum, Baross u. 13, H-1088, Budapest, Hungary.

MALACOLOGICAL REVIEW, SUPPLEMENTS 1 AND 2. – Supplements 1 and 2 are available from *Malacological Review* at the prices given below. They can be ordered from *Malacological Review*, P.O. Box 2750, Ann Arbor, Michigan 48106, U.S.A.

Supplement 1. *Freshwater snails of Taiwan (Formosa)*, by Gary L. Pace. This illustrated monographic study deals with the identification, classification, distribution, zoogeographic affinities and parasitological importance of thirty-nine species of Formosan freshwater gastropod mollusks. US$15.00, postpaid.

Supplement 2. *The Mekong Schistosome*, J.I. Bruce, S. Sornmani, H.L. Asch & K.A. Crawford, Editors. This publication is a monograph on the newly discovered human blood fluke, *Schistosoma mekongi*, and its unusual molluscan host, *Tricula aperta*. In addition to details on the parasite, this book presents various studies on the snail intermediate host, including its anatomy, systematic and zoogeographic relationships, evolution, habitats and bionomics, laboratory maintenance and culture, susceptibility to the parasite, effect of the parasite on the snail, the snails' role in disease transmission, and sensitivity of the snails to molluscicides. US$26.00, postpaid.

WESTERN SOCIETY OF MALACOLOGISTS, 1982 ANNUAL MEETING. – The Western Society of Malacologists will hold its 15th Annual Meeting at the University of Redlands, Redlands, California, from 20-23 June 1982. Symposia are being planned on the Eastern Pacific Bivalvia and Muricidae. In addition, a photography work shop will be held. For further information, please contact: Ms. Kit Stewart, 19 Lan Rancheria, Carmel Valley, California 93924, U.S.A.

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CONTENTS OF CURRENT SERIAL PUBLICATIONS ON MOLLUSKS

The contents of current malacological serial publications, as shown by their tables of contents, are herewith reproduced as a service to our readers. The publications are listed in alphabetical order. Also listed are the locations of the editorial offices. Those publications that do not have their contents printed in this current issue of *Malacological Review* are marked by an asterisk in the right hand column below; contents of these publications will be included in future issues of *Malacological Review*.

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Archiv für Molluskenkunde

der Senckenbergischen Naturforschenden Gesellschaft
Organ der Deutschen Malakozoologischen Gesellschaft

Begründet von Prof. Dr. W. Kobelt
Weitergeführt von Dr. W. Wenz und Dr. F. Haas
Herausgegeben von Dr. R. Janssen und Dr. A. Zilch

Arch. Moll. 111 (1980) (1/3) 1-163 Frankfurt a.M., 20. 3. 1981

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ANNONCE AUX SOUSCRIPTEURS ET AUX AMIS DU JOURNAL DE CONCHYLIOLOGIE

A mon très grand regrèt, je dois arrêter la publication du Journal de Conchyliologie. Le présent fascicule No. 4 du Volume CXV sera le dernier.

Il est de plus en plus difficile à une publication privée, non subventionnée et, sans but lucratif, de surmonter les conditions liées à des formes nouvelles de vie et d'économie.

Le Journal de Conchyliologie ayant pour seul but l'avancement de la Science a toujours été classé comme publication "sans but lucratif". Pour que sa balance budgétaire ne comporte aucun bénéfice, il a toujours fallu, en fait, supporter un déficit, petit ou grand, au détriment des éditeurs. Cette situation s'est aggravée avec les nouvelles conditions de l'économie.

D'où la décision à laquelle je me vois obligé.

Je souhaite que la nouvelle génération des malcologistes français puisse publier un périodique similaire, mais il est évident que, pour le Journal de Conchyliologie dans sa formule traditionnelle, c'est vraiment la fin. Tels sont les impératifs de notre époque.

Le Journal de Conchyliologie est l'un des plus anciens périodiques existant, et le plus ancien périodique malacologique du monde. Il est hautement regrettable qu'il doive arrêter sa publication.

On peut dire du moins qu'il a rempli son rôle pendant une très longue période, 130 ans, grâce à l'effort constant et complètement désintéressé de mes prédécesseurs comme de moi-même. Je regrette de ne pas pouvoir le faire vivre plus longtemps.

P.-H. FISCHER.

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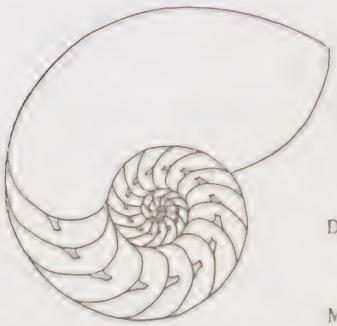

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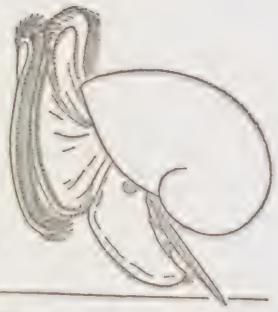

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